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The Ecology of the Ants of the Welaka Reserve, Florida (Hymenoptera: Formicidae). Part II. Annotated List

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In the following annotated list, the discussion of every ant form has been arranged so that topics appear in the same order. Any points of taxonomy which are felt to be important are discussed first. The distribution through plant associations, strata, and nesting sites, is listed next. Comparisons are made with the ant's distribution in Gainesville or other regions, or with another ant on the Reserve which may replace it in some of the plant associations, if such a discussion is felt necessary for a better understanding of the habits of the ant. Notes as to its life history are followed by others on its activity. Miscellaneous remarks are added in a final paragraph.

As indicated in the introduction,[1] the taxonomy of the ants in the present study is based on Creighton's recent work (1950) in which he reduced the quadrinomial system, prevalent until 1950 in the family Formicidae, to the trinomial system used in the dynamic view of nomenclature. Any departure from the names which Creighton uses is explained in the text of the Annotated List under the ant concerned. Some forms were found during the study which could not be definitely identified. Such forms that were recognizably different are listed, and comments are made concerning their taxonomic status.

In presenting the life history data, an attempt was made to determine an average number of workers present in a flourishing colony of each ant form. In some cases this has been impossible, or has been derived from the counting of only one nest. In addition, the seasonal appearance of immatures, males and females is indicated for each form.

Structural measurements have all been made from the lateral view. Total length is the sum of the distances from the base of the mandibles to the back of the head, from the most anterior part of the pronotum to the base of the propodeum through the abdominal pedicels, and from the anterior to the posterior of the abdomen. All measurements were the shortest straight lines covering the given distances.

Fourteen ant forms were taken during the present study which had not been recorded from Florida. They are as follows: *Proceratium*, near *silaceum; Aphaenogaster treatae; Pheidole pilifera; Crematogaster coarctata vermiculata;*

[1] For preliminary remarks and ecological interrelationships, see Van Pelt, 1956.

Solenopsis minutissima ?(see annotated list); *Myrmecina americana; Leptothorax texanus davisi; Smithistruma bunki; S. clypeata; S. creightoni; S. ornata; S. pulchella; S. talpa; Paratrechina arenivaga.*

Several ant forms taken in the Gainesville Region were not found during the present study on the Reserve. These are as follows: *Eciton carolinense; Sysphincta pergandei; Ponera coarctata pennsylvanicus* (*lit.*); *Crematogaster minutissima minutissima* (det. ?); *Monomorium pharaonis; Xenomyrmex stolli floridanus; Leptothorax bradleyi; L. wheeleri; Tetramorium simillimum* (lit. from Sanford, Jacksonville); *Lasius alienus americanus; Formica schaufussi dolosa* (lit.). Other ants taken in Welaka, but not in Gainesville are: *Amblyopone pallipes; Proceratium,* near *silaceum; P. croceum; Ponera ergatandria; Aphaenogaster macrospina; A. treatae; Pheidole dentigula; P. pilifera; Cardiocondyla wroughtoni bimaculata; Solenopsis minutissima* ?; *Myrmecina americana; Leptothorax texanus davisi; Smithistruma bunki; S. clypeata; S. dietrichi; S. ornata; S. pulchella; S. talpa; Formica archboldi.* The following ants, taken within seventy miles of the Reserve, have been cited in the literature: *Pheidole megacephala* (St. Aug.) (not listed by Creighton, 1950); *P. anastasii* (Sanford); *Leptothorax curvispinosus* (Jacksonville; pinned specimen); *Tetramorium simillimum* (Sanford; Jacksonville).

Family FORMICIDAE
Subfamily DORYLINAE

ECITON NIGRESCENS (Cresson)

On July 5, 1948, the single collection of *nigrescens* made on the Reserve was recorded for mesic hammock. The nest was under litter which had gathered in the center of the base of a stump rotted so that only the rim was left standing. The nest extended into the stump, but the major portion was in and under the moist litter in the stump and in the nearby chambered sand.

All of the workers were huddled in a tight ball. No activity was observed until the workers were disturbed, but then the workers ran hurriedly in all directions. No individuals of the reproductive caste were seen, even though the nest was dug into, and returned to later.

Cole (1940) made some observations concerning the nesting habits of this ant in the Great Smoky Mountains. Two colonies he found there were beneath large, flat stones, loosely applied to the soil, in open grassy areas . . . . Deep within the soil the ants occupied large brood-filled chambers constructed around imbedded and partially decayed tree roots . . . . The soil, even at chamber level, was dry and firm.

ECITON OPACITHORAX Emery

E. opacithorax was found occasionally in longleaf pine flatwoods. All nests were under the bark and loose wood of stumps or logs, and extended into nearby litter. All logs from which this ant was taken were longleaf pine (*Pinus palustris*). In stumps the ant occupied all available space under the bark and all suitable crevices; in logs the ant nests were several feet long.

One nest in a stump was estimated to contain between 40,000 and 50,000 workers. These numbers were obtained by placing all the ants in vials, counting the number in one vial, and measuring this vial against all the others.

Numerous individuals of *Eciton* were taken at the openings of a nest of *Solenopsis geminata* in the sand one and one-half feet from a stump in which the colony of *opacithorax* was located. The *Eciton* nest abutted a nest of *Brachymyrmex depilis*, and partially occupied a nest of *Crematogaster clara* in the stump. Groups of *Eciton* were also taken from termite galleries in the stump. *Leptothorax pergandei floridanus* and *Aphaenogaster macrospina* were found wandering near the stump. The following animals were taken through the Berlese funnel from the litter of the *Eciton* nest: beetle larvae; round worms; heads and thoraces of *Odontomachus haematoda insularis; Solenopsis molesta; Proceratium croceum;* dealated female of a species of *Solenopsis* (*Diplorhoptrum*); wasp of the family Bethylidae (?). From another nest the following were taken: *Brachymyrmex depilis; Paratrechina parvula;* diplopods.

A large portion of a colony with its nest litter was placed in a large lard can and brought into the laboratory. To prevent the escape of the individuals, the lard can was placed on a platform surrounded by water. Very few workers, however, were observed wandering on the platform, although workers carefully placed the dead or injured individuals in a pile outside of the lard can on the platform.

Subfamily PONERINAE

AMBLYOPONE PALLIPES (Haldeman)

Previous to Brown's paper (1949), *pallipes* was considered a species of *Stigmatomma*. Brown, however, has given reason to place *Stigmatomma* as a subgenus of *Amblyopone*. It is treated as such in this paper.

One collection of *Amblyopone* was made during April in bayhead. Several ants were gathered in moist litter near and in fern roots. A careful examination of the roots and litter nearby revealed no additional specimens.

Cole (1940) has the following to say concerning this species in the Great Smoky Mountains:

> The nest consists of one or two openings beneath or beside a stone or under the topmost forest litter. Almost perpendicular galleries connect with small subterranean chambers never far beneath the surface. . . . These ants are nowhere abundant in the Park but seem to occupy rather circumscribed areas where environmental conditions, particularly moisture and deep shade, are favorable. Colonies were most numerous in second-growth pine woods.

The collection on the Reserve, made on April 22, 1949, yielded one male. The workers are very reclusive, and quickly find crevices in which to hide. Their color blends with that of the soil and duff. Haskins (1928) has reported on the behavior and habits of this ant.

PROCERATIUM CROCEUM (Roger)

P. croceum was collected occasionally in longleaf pine flatwoods and rarely in bluejack oak. All of its nests were taken in the surface stratum from fallen longleaf pine logs. These logs were either moist or wet, with

the wood pulpy or soft and separable between the annual rings. The nests extended toward the center of the log.

Two colonies were counted. One contained 24 workers, 12 callows, and 1 male. The other, seemingly complete, had only 3 workers. There was a queen in each of these nests and no immatures were noted. The male was taken on November 23, 1949. It was found about two feet from the nest, and since no other males were taken, it is possible that a flight had recently taken place. Workers of *croceum* were sluggish in their movements, while the male was alert and moved quickly.

Cole (1940) indicates that his single collection of this species in the Great Smoky Mountains was made in a wet, dense area of mixed cove hardwoods. He adds that the log in which the ants were found was easily broken apart into firm, wet pieces. The nest was "well toward the center of the log, in the more firm core wood" and had "small galleries and chambers chiefly with longitudinal penetration. In all the nest covered a length of [only] about 4 inches . . . . The colony was rather small, being composed of about 30 workers." In the Chicago area, Gregg (1944) records the presence of this species beneath dung.

PROCERATIUM, near SILACEUM Roger

From Emery's redescription of *Proceratium silaceum*, the form dealt with here seems to be close to this latter species. However, M. R. Smith, to whom specimens were sent would not place the form beyond genus. In an attempt to revise the genus he found (communication) that "The previously mentioned characters for separating the two species did not appear dependable and I could not discover any new characters that were any good either." Thus the form is given an uncertain taxonomic status.

One collection of this form was made on October 17, 1948, from the base of a slash pine. The colony was nesting in bark buried under the soil surface. Six individuals were taken. As in *P. croceum*, the workers are sluggish in their movements.

EUPONERA GILVA (Roger)

E. gilva was confined in its distribution to the moist or wet hammock areas. It was taken once in mesic hammock, and occasionally in hydric hammock.

Its nesting sites were in fallen logs. A typical nest extended for two and one-half inches in debris under the bark of a log. Specimens have also been taken from litter, and from the debris decomposing between the rootlets in and under the litter.

A nest from hydric hammock contained 26 workers and one queen. The eggs, larvae (which are well equipped with body spikes), and pupae were observed in separate places in the nests, with the pupae usually more toward the surface, or toward the outside in log nests. Since so few nests were seen, no further life history data were obtained.

Although the ants are slow in their movements most of the time, they are quick to find concealment. Their elusiveness is increased by their color

which is similar to that of the wood where they live, and by their ability to hide motionless in every narrow crevice.

Smith (1934) records *E. gilva* from Mississippi, Alabama, and Tennessee. His observations on the nesting sites coincide with the above. He states that its nests "in some instances contain as many as from one to several hundred workers and often as many as ten or more dealated queens." He remarks further that Creighton found fully developed males and a winged female on June 20 in southern Alabama.

PONERA ERGATANDRIA Forel

Mention needs to be made of a number of small specimens of *P. ergatandria* collected on the Reserve. These workers are in all measurements more diminutive than specimens taken in Dade County, Florida, and are likewise smaller than other *ergatandria* taken on the Reserve. While the latter specimens fit the description of *P. ergatandria* which Smith (1936) gives, the smaller workers from the Reserve differ in total body length. Smith lists the body length as 2.3-2.9 mm.; the smaller workers on the Reserve measure only 2.0-2.1 mm. Moreover, the ventral portion of the petiolar tooth is smooth in the larger specimens, and serrate in the smaller specimens. Smith (communication) says that he has noted much variation in the workers of *ergatandria*, and considers all of the specimens from the Reserve as of that species. The smaller specimens have been found only in mesic and hydric hammocks, whereas the larger specimens were spread mainly over drier areas. Both variants will be treated together in the following discussion.

P. ergatandria colonies were taken occasionally in hydric hammock and mesic hammock; and rarely in turkey oak, bluejack oak, and black pine-fetterbush flatwoods. A typical nest was taken from under the moss near the base of a living oak tree in hydric hammock. No life history data were obtained.

PONERA OPACICEPS Mayr

A discussion concerning the variation in the shape of the petiolar scale in *P. trigona opacior* and in this form can be found under *P. t. opacior*. Many of the nests of *opaciceps*, especially in marsh, contained one to several individuals which are evidently aberrant workers. These insects have large compound eyes, comparable to those of the queen, and the petiole is more slender than that of the normal worker. It is perhaps significant that queens were not found in nests which contained these aberrant forms.

This species prefers the wet or flooded areas of the Reserve, and tends to replace *P. trigona opacior*, a form which prefers high, dry areas. It has been taken abundantly in marsh; commonly in hydric hammock and river swamp; and rarely in Rutledge slash pine flatwoods, bayhead, and xeric hammock. In the Gainesville region, *P. opaciceps* was taken in longleaf pine flatwoods where there are more fallen logs than in the same plant association on the Reserve. It ought to occur also in at least the lower portions of mesic hammock.

Most often this ant nests in the bases of sawgrass plants between the appressed leaves. Many times the ant can be found in the wet or saturated

moss-covered stumps of the plants where there is an intermingling of roots in the decomposing, appressed leaves and wet debris. The other nesting sites, in order of preference, are: 1) fallen logs, 2) dead stumps, 3) bases of living trees (under moss and litter at water surface), 4) in litter (wet), 5) palmetto roots on ground, 6) under mat of palmetto roots, and 7) under mat of palmetto trunks. In general, the nests are wet to saturated and built in debris. Most of the nests, especially those in sawgrass, are at the water surface, or just above or below it. (In this latter case, the tight growth of the plant parts seems to keep the water from the nest.) In situations which are less wet, the insect continues to simulate the above-mentioned nesting conditions in its choice of wet pulpy wood of logs, or the debris found under the bark of logs or stumps.

Of 5 nests counted, the number of workers varied from 15 to 84, with an average of 40 per nest. Each of these nests contained from one to three of the aberrant workers described above, and none contained a queen. Immature forms probably occur in all months, but from September through November very few were noticed in the nests. Females are produced from September to November, and males from October to November.

This is a fast moving and evasive ant which blends with the color of its surroundings. It is much less active in winter months, although this is the period winged forms are in the nest.

PONERA TRIGONA OPACIOR Forel

An examination of specimens of this form and of *P. opaciceps* in the Museum of Comparative Zoology seemed to indicate an overlapping variation in the petiolar scale of the two forms. On the basis of the character of the shape of the petiolar scale used by Smith (1936), specimens labeled *opacior* were more like *opaciceps*. Perhaps the shape of the petiolar scale will be found dependent on environment, and therefore of no use as a key character. It is probable, however, that, since the specimens collected on the Reserve fall into two distinct groups, misdetermination has been involved in the museum collection.

In all respects except total length, the Welaka specimens agree with Smith's description in which he cites the length of workers of *opacior* as 2-2.3 mm. Workers from the Reserve measure 2.4-2.7 mm in total length.

P. t. opacior tends to prefer the higher, drier plant associations. It was taken commonly in xeric hammock; occasionally to commonly in turkey oak; occasionally in bayhead and Plummer slash pine flatwoods, in all well-drained areas except Pomello scrubby flatwoods, and in the hammocks; and rarely in the other flatwoods stations. No collections have been made from Pomello scrubby flatwoods or the seasonally flooded areas of the river swamp and marsh. Cole (1940) points out that in the Great Smoky Mountains the ant does not nest in dense wet woods, but prefers rather open areas where the soil is able to contain an appreciable amount of moisture.

The majority of the nests occupied the surface stratum. The several nests recorded from sand, moreover, did not extend more than a few inches into the sand, but were mostly under litter. The nests in the

surface stratum were usually associated with debris, although some nests were found with little or no debris. Several of the nests taken in fallen logs were found under the bark against fairly hard wood. The order of preference of nests in the surface stratum is: 1) fallen logs, 2) dead stumps, 3) bases of living trees, 4) litter, 5) palmetto roots on ground, 6) under mat of palmetto roots, and 7) under mat of palmetto trunks.

Of four nests taken from wood, the number of workers varied from 7 to 21, with an average of 13. None of these nests contained queens. Immature forms have been found in all months. Males have been observed in flight in December and February. No information has been obtained concerning females.

P. t. opacior is relatively fast moving, and characteristically evasive. Individuals are difficult to see because they are very nearly the color of the wood or litter surrounding their nests. They seek immediately the first available crevice in which to hide.

Nests are occasionally found in the same logs and stumps as nests of *Odontomachus haematoda insularis*.

LEPTOGENYS ELONGATA MANNI Wheeler

Creighton (1950) lists the range of this ant as "southern Florida." It has, however, been taken on the Welaka Reserve, as well as in Gainesville, thereby extending the range listed by Creighton.

On July 26, 1950, a single specimen of this Ponerine was collected in river swamp. The swamp at the time of collection was extremely dry, and the ant was crawling over litter that contained very little moisture. In the Gainesville region, *L. elongata manni* was taken from mesic hammock in rotting stumps.

ODONTOMACHUS HAEMATODA INSULARIS Guerin

O. h. insularis is a widespread ant on the Reserve, and is well represented in nearly all of the stations except marsh, where it has not been found. It occurs abundantly in black pine-fetterbush flatwoods and mesic hammock; commonly to abundantly in turkey oak and hydric hammock; commonly in Leon scrubby flatwoods, longleaf pine flatwoods, Plummer slash pine flatwoods, xeric hammock, river swamp and bayhead; and occasionally in bluejack oak, scrub, Pomello scrubby flatwoods, and Rutledge slash pine flatwoods.

A majority of its nests have been found in sand, almost always under litter or logs. The remainder of the nests were taken in the surface stratum. Where there are suitable logs or stumps present, this ant shows no preference between wood and sand. However, on the Reserve, because of the existence of relatively few suitable logs or stumps, the most favored nesting site was in sand under litter. In the Gainesville region most of the nests of *O. h. insularis* were taken in logs.

Beginning with the most common, the nesting sites of *O. h. insularis* in Welaka are: 1) under litter, 2) under logs, 3) in and under logs, 4) in dead stumps, 5) in fallen logs, 6) under mat of palmetto trunk, 7) in litter, 8) in bases of living trees, and 9) open sand or with very light

litter. Most nests in logs and stumps were in wood of an advanced stage of decay, although nests were found in wood in all stages. There was no preference between pine and broad-leaved wood, but all nests were wet or moist. Charred wood was not rejected. Many of the nests in logs and stumps, and under logs, ramified into chambers in the nearby sand. In the black pine-fetterbush association, several nests were found among the roots of fetterbush.

On several occasions *O. h. insularis* has been found in the same stump or log with *Camponotus abdominalis floridanus*, but the association probably depends on a common suitable nesting site. Both of these ants sometimes extend their nests into sand near the wood which contains the major portion of their colonies. Both, moreover, live under logs, but *O. h. insularis* sometimes lives in sand alone. The chambers of these large ants are never very deep, and usually appear to be ready-made cavities into which the ants moved. They have not specialized in excavating to the degree that the true crater forms have. Many of the passageways, too, seem to have been constructed by some other agent than the workers, since they are in most cases much too large for the size of the ant. The portions of the nests in sand are commonly supported by humus and leaf litter.

Large nests of *O. h. insularis* have not been seen on the Reserve. One nest, perhaps slightly smaller than average, contained 20 workers and 3 callow workers. Immatures have been observed in the nests in all months, but not during cold periods. On numerous occasions males have been taken in flight and in the nests from May through early August, but no information has been gathered concerning the females.

When the soil is saturated during the summer rainy season, the workers often bring their immatures to the surface and place them under leaves. Single workers also can be seen resting under the cover of a leaf during these periods, as well as during the colder months of the year.

This ant is one of the most conspicuous in a majority of the plant associations on the Reserve. It is quite active above ground, especially during the warmer months, and large workers, foraging alone, are commonly seen. In the cold periods, however, activity, both above ground and in the nest, is reduced to a minimum, and its absence above ground is quite noticeable.

O. h. insularis is known to feed on insects. When large insects are caught, several workers cooperate in carrying the intact bodies to the nest opening. Workers have been attracted to the peanut butter and oatmeal bait used in mammal traps.

Insects which have been found living near *O. h. insularis* in the same log or stump are: *Camponotus abdominalis floridanus; Paratrechina parvula; Reticulitermes* (*flavipes?*) (Isoptera).

In several instances mites have been found clinging to workers. They have been found on all parts of the body, but especially on the head, gaster, and propodeum.

Foraging workers have been found in association with several other species of ants. Neither the *Odontomachus* nor the other ants were much disturbed. In one instance an *Odontomachus* worker was very inquisitive concerning the activities within the crater of a nest of *Trachymyrmex septentrionalis seminole*. The worker repeatedly ran to the nest opening with waving antennae, but neither the visitor nor the *Trachymyrmex* gave much attention to the other.

Subfamily PSEUDOMYRMICINAE

PSEUDOMYRMEX BRUNNEA F. Smith

P. brunnea nests were taken occasionally in turkey oak, Leon scrubby flatwoods, Pomello scrubby flatwoods, mesic hammock, hydric hammock, river swamp, and marsh; rarely in scrub, Rutledge slash pine flatwoods, xeric hammock, and bayhead. The ant shows a preference for river swamp, hydric hammock, and the dense Pomello scrubby flatwoods. On the other hand, it has been collected only once in any type flatwoods other than the scrubby flatwoods. *P. brunnea* thus replaces *P. pallida* in the wet or seasonally flooded areas, whereas *P. pallida* replaces *brunnea* in the flatwoods areas. The difference can be attributed to the fact that *pallida* is able to live in tall grass stems, whereas *brunnea* is not. Moreover, *brunnea* prefers the more dense, wet woods, and *pallida* the more open areas.

Almost all of the colonies of *brunnea* have been collected in the arboreal stratum. Nests have been equally divided between true twigs and small branches. A single collection from the herbaceous stratum was made six feet above the ground in a flower stalk of a sawgrass plant.

Two large nests of this species were taken, one with 79 workers and 1 queen, the other with 79 workers and 8 queens. Other nests contained 18 workers and 1 queen; 9 workers and no queen; and 7 workers and no queen. A mating flight occurred on June 17, 1950, and winged forms were observed in previous years from June through September. Immature forms occur in the nests almost all year, and usually there are a large number of larvae, e.g., 30 to 65 large larvae and many more small ones.

P. brunnea is agile and is able to disappear easily on the other side of a branch. It seems to prefer foraging when temperatures and humidity are high.

PSEUDOMYRMEX PALLIDA F. Smith

Until Creighton's paper (1950), *P. pallida* and *P. flavidula* were recognized as separate species on the basis of the presence or absence of black spots on the base of the abdomen. Creighton has synonymized *flavidula,* since he has found that a nest series of sufficient length will contain individuals with and without black spots on their gasters. Nest series from the Reserve also have shown these characteristics.

P. pallida was found in eight stations. The black pine-fetterbush association affords a great many *Andropogon* stems which are suitable nesting places for *pallida.* As a consequence, the ant is found abundantly in this station. It occurs commonly in longleaf pine flatwoods and Leon scrubby flatwoods; occasionally in the sandhill areas and the slash pine flatwoods; and rarely in xeric hammock.

Because of its preference for tall grass stems as nests, *P. pallida* was found most often in the herbaceous stratum, but was also taken arboreally. It was absent from the other strata.

The nesting sites of *pallida* were almost always true twigs or were twig-like. All but a few collections were made from tall grass; a few others were made from the twigs of pine and scrub oaks; and the ant can often be

found nesting in the stems of planted bamboo. Several collections were made from twig-like small branches.

Of 12 colonies taken, the number of workers varied from 5 to 25, averaging 11. Of these colonies 7 contained no queens. (These small, queenless aggregates may really be sections of a larger group centered around a queen. See *Crematogaster ashmeadi* and *C. minutissima missouriensis*.) Eggs, larvae, and pupae are present in all months, with a peak of abundance indicated in August. Winged forms were taken from the nests from August through November. No nest contained both males and females.

This agile ant has a knack of disappearing behind a grass stem or a twig when disturbed. When a nest is broken open, many of the ants will remain perfectly still until touched. Normally they exhibit a moderate to considerable above-ground activity. Several workers were found, evidently foraging, within a cocoon of a dead bagworm (*Thyridopteryx ephemeraeformis* Haworth) hanging from a fetterbush.

The eggs, larvae, and pupae of this ant are usually more or less segregated. A typical nest contained eggs and some larvae in the base of a grass stem, other larger larvae near the middle, and pupae and a few eggs near the top of the stem. Many times the queen is found near or at the top of the stalk.

As the *Andropogon* dies in the fall and the stems become drier and less habitable, the ants are forced down near or into the base of the stems, or into portions of stems that have been broken from the plant but which are still supported by vegetation. Their abundance becomes somewhat less until the spring growth of grass creates new nesting sites. In this respect these ants, like *Paratrechina parvula* in marsh, show a seasonal variation in occurrence which is dependent on the seasonal variation in occurrence of the nesting site plant.

It might well be pointed out that the nature of the *Pinus serotina-Desmothamnus* association, which this ant occupies in the most abundance, gives an advantage to these grass stem ants in the summer, just as it creates a disadvantage for the ant when the Andropogon dies in the winter. During the height of the rainy season from early July into August, the water level may reach within inches of the soil surface, or even exceed it. Deep burrowing forms which cannot withstand prolonged periods of submergence will be kept at a minimum or eliminated. A few forms, such as *Irodomyrmex pruinosus* and *Formica archboldi*, can withstand the submergence of their lower galleries, and undoubtedly fluctuate the depth of their galleries with the rise and fall of the water table. The grass stem ants, on the other hand, remain relatively unaffected by the water level change, are free of competition for their nesting site, and at the same time are adapted to procure the above-ground food supply.

Subfamily MYRMICINAE

POGONOMYRMEX BADIUS (Latr.)

P. badius is one of the most restricted ants of the Reserve as far as occurrence in plant associations is concerned. It requires open areas in which

to build its dome-shaped mound, and only a few situations suitable in this respect occur in the stations studied in the present problem. Xeric hammock is preferred and nests are found there commonly. *P. badius* nests were taken occasionally to commonly in turkey oak, and occasionally in bluejack oak. Many nests are found on lawns, around gardens, and in firelanes. All of its nests were complete, domed craters. Characteristically, the areas around the openings of the nests are always bare of vegetation in well-established colonies. Many of these areas are edged with charred pieces of wood, seeds, twigs, and other debris. The charcoal rim of many of these mounds is a conspicuous feature of the nests. Wray (1938), giving an account of the ant in North Carolina, mentions that nests in that region have the same features. He also gives a description of the internal structure of the nests.

The active ant carries on its most vigorous activities in rather low relative humidity (below 55%), and in high temperature (35-40° C., or slightly above). Winged forms have been observed in the nests in May, and mating flights were recorded for June.[2]

The following seeds were taken from nests of *Pogonomyrmex badius*: *Ampelopsis arborea*,[3] *Phytolacca rigida*, *Pinus* sp., *Cenchrus gracillimus* (sandspur), *Sabal palmetto* (cabbage palm), *Diodella teres* (buttonweed), and centipede grass.

The ants were able to carry all of these seeds except those of the cabbage palm. One of the latter seeds presented somewhat of a problem, although the ants were able to carry it for short distances in their mandibles. When they had transported it to the mound, several ants began digging under it with their forelegs until a crater was formed with the seed in the center. When the seed was removed for identification, the crater was becoming deeper and the ants were making no progress. It was observed that ants can carry seeds for at least 100 feet. Cole (1932), however, notes that *Pogonomyrmex occidentalis* in the western United States carries seeds for as much as 1.35 miles.

APHAENOGASTER ASHMEADI Emery

A. ashmeadi prefers the areas of the Reserve which offer xeromesic conditions in the subterranean stratum. It is found occasionally to commonly in xeric hammock and Leon scrubby flatwoods; occasionally in bluejack oak, scrub, and mesic hammock; and rarely in turkey oak and bayhead.

A. ashmeadi is confined to the subterranean stratum. In all cases it nested in sand, and most of its nests were under litter. One nest, situated where there was no litter, had no recognizable crater and two nest openings.

The size of the nest is approximately the same as the closely related *A. treatae*. One nest contained 326 workers, 7 callows, 250 pupae, plus eggs, larvae, and a queen. Winged forms have been found in the nests in June.

The above-ground activity of this ant is moderate to considerable on clear, sunny days when the relative humidity is below 70%. It has not been taken

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[2] For more complete data, see Van Pelt (1953).

[3] Determinations of all seeds were made by A. M. Laessle, Department of Biology, University of Florida.

foraging when the temperature was below 20° C. Along with other ants, *A. ashmeadi* shows a tendency to become very inactive above ground during the winter. The form is carnivorous, and is attracted to raw liver; it has been seen carrying dead ants of other species, especially *Odontomachus haematoda insularis*.

APHAENOGASTER FLORIDANA M. R. Smith

A. floridana was taken occasionally in turkey oak on the Reserve. In the Gainesville region, it was also taken in ruderal situations, such as open, sandy roadsides. Nests are either complete craters or rudimentary craters around small clumps of grass.

A. floridana is a fairly fast moving insect. Most of its foraging is done at night, but it is sometimes active during the day, especially during overcast weather. It is attracted to molasses traps.

APHAENOGASTER FULVA Roger

Within a given nest of *fulva* there is great variation in character proportions of the workers from the incipient to the mature colony. Of the specimens sent him from the Reserve, Dr. Smith (communication) says, "The smaller workers with more posteriorly rounded heads and longer antennae probably belong to young colonies. As the colonies increase in size the later workers acquire shorter antennae and less rounded heads." Because of this change in characteristics, it is important to recognize workers of an incipient colony, so that they will not be misidentified as a closely related form.

It can be mentioned here that individuals with shorter spines, keying to *rudis* in Creighton's paper (1950), have been found on the Reserve, but are not included because of their small number and uncertain taxonomic position.

A. fulva prefers the lower areas of the Reserve. The species has been taken commonly in river swamp; occasionally in scrub, longleaf pine flatwoods, hydric hammock, and bayhead; and rarely in Rutledge slash pine flatwoods, xeric hammock, and marsh. It tends to replace *A. ashmeadi* in the wetter areas.

Ants of this group have been found in both the subterranean and surface strata. Nests were equally abundant under logs, in litter, in fallen logs, under the mat of palmetto roots and trunks, and in dead stumps. They also have been found in and under logs and in the bases of living trees. Logs which contain nests are usually in the last stages of decay. One nest was between the bases of palm fronds and the trunk of the palm in the debris gathered there.

Of the 2 nests counted, the one from scrub contained 46 workers, 10 worker pupae, and 1 queen, while the other from river swamp contained 65 workers, 3 callows, 15 worker pupae, and 1 queen. Immatures were in almost every nest collected. Males were found in the nests from May through July; no information was obtained concerning the females.

The ants of this group are quite active. The workers are attracted to a mixture of peanut butter and oatmeal. They have been noted living next

to nests of termites (*Reticulitermes flavipes*), and have been seen carrying live termites in their mandibles.

APHAENOGASTER LAMELLIDENS Mayr

Only one collection of *A. lamellidens* was made on the Welaka Reserve. This nest, in xeric hammock, occurred in the base of a broken limb which had decayed differentially. In the Gainesville area, the author has collected the species in mesic hammock in fallen logs. In the Great Smoky Mountains, Cole (1940) has found a few colonies "in wet rotting logs in a deeply shaded forest."

Although collections in other regions indicate that *lamellidens* occurs usually in the surface stratum, its collection on the Reserve from the stump of a limb 5 feet above the ground places it in the arboreal stratum.

APHAENOGASTER MACROSPINA M. R. Smith

A. macrospina was taken occasionally in bluejack oak, longleaf pine and Rutledge slash pine flatwoods. All of its nests were in the subterranean stratum under litter. Its distribution on the Reserve shows a preference for pine growths.

This is a moderately active ant. On a number of occasions, it has been attracted to molasses. One nest counted contained 65 workers, 10 worker pupae, and 1 queen. Attention was drawn to the nest by the capture of individuals of this species in a molasses trap. Part or all of the 44 ants caught in the molasses trap may have belonged to this colony.

APHAENOGASTER TEXANA Emery

A. texana nests occasionally in scrub, and rarely in longleaf pine flatwoods, xeric hammock, and mesic hammock. Nests have been taken only from the surface stratum in wet to saturated logs in the last stages of decay. The habits of this species are much the same as those of *fulva*.

APHAENOGASTER TREATAE Forel

Nests of *A. treatae* have been found occasionally in Leon scrubby flatwoods, and rarely in scrub. Although it has been found in only these two plant associations, there is no apparent reason why it should not occur in other areas with relatively light leaf litter, as does *A. ashmeadi*.

All of its nests have been found in the subterranean stratum under litter. One nest contained eggs, 20 larvae, 81 pupae, 20 callows, 292 workers, and 1 queen. Two diplopods were removed from the dirt surrounding the nest.

A. treatae is a moderately fast moving, timid insect. Workers have been noted carrying larvae of various kinds into the nests. A grasshopper nymph was readily eaten when introduced into a nest transplanted into the laboratory.

This laboratory nest consisted of the queen and three workers. The queen laid eggs within three days of the time that she was placed in the nest. All of these eggs were kept near a damp sponge in the nest, and were cared for

by the workers. The queen rested *on* the sponge, and paid little attention to the clump of eggs.

A. treatae has been taken from the Chicago area (Gregg, 1944) and from Iowa (Buren, 1944), and Cole (1940) has the following to say concerning nests in the Great Smoky Mountains: "Invariably, it was found colonizing open woods (usually pine) or less frequently grassy fields and slopes. All nests were beneath stones of varying size, and each nest possessed a single entrance, either beneath or beside the stone, leading by a gallery to a series of large interconnected chambers deep in the soil . . . . In all cases, however, the soil was rather moist." It is probable that the "open woods" and "grassy fields and slopes" of the Great Smoky Mountains offer conditions similar to the open areas of the Reserve. Since there are few stones on the Reserve, the ant here must be satisfied to use leaf litter to cover its nest opening.

PHEIDOLE DENTATA Mayr

Ph. dentata nests are well represented in all of the stations on the Reserve except marsh. It was taken most often in the better drained areas, as well as the hammocks, river swamp, and black pine-fetterbush flatwoods. Colonies occur abundantly in scrub, Leon scrubby flatwoods, Pomello scrubby flatwoods, and river swamp; commonly to abundantly in bluejack oak, xeric hammock, mesic hammock, and black pine-fetterbush flatwoods; commonly in turkey oak, longleaf pine flatwoods, Plummer and Rutledge slash pine flatwoods, and hydric hammock; occasionally in bayhead; and rarely in marsh.

Over two-thirds of the *dentata* nests taken were on the soil surface, and with the exception of one collection from a small branch, all others were taken from sand, mostly under litter. Nests under litter, and nests in logs and stumps are preferred by *Ph. dentata*. The other nesting sites in which it was found, in order of importance for the ant, are: 1) in litter, 2) under mat of palmetto root and stump, 3) in bases of living trees, 4) under logs, 5) in and under logs, 6) in grass clumps, 7) open sand (rudimentary craters), 8) palmetto root on ground, and 9) in small branch. Other collections were made under moss on a saw palmetto root, and several records were made of nests in fern roots.

In Gainesville, *Ph. dentata* was found to nest equally often in logs and in rudimentary craters. On the Reserve, probably due to the presence of litter and at least some wood in almost all situations, craters of this ant were seldom found. Even though other ants, such as *Pogonomyrmex badius* were able to build crater nests only, *Ph. dentata* showed its preference for nests in wood or under cover of wood or litter, by avoiding the open areas.

Nests were recorded in wood in all stages of decay, and in wood that varied from wet to dry. Most of the nests in logs or stumps were in pine, although a number were found in broadleaved wood. Often these nests were under the bark, but a few nests in stumps extended down into the root systems. During the wet seasons, nests have been found several feet high in dead tree trunks.

Nests of this ant usually contain a large number of individuals. One rather small nest comprised 162 workers, 9 soldiers, and 1 queen. Immature forms are present all year except during cold periods. Winged forms have

been taken in flight in May and June, and a dealate female was recorded wandering in February. Reproductive form pupae were seen in the nests in April.

Many times, especially during the rainy season when the ground becomes very wet, the immatures are brought to the surface and laid on or between leaves. On other occasions, in log nests, the immatures were scattered throughout the log without any seeming order. Similar nests, however, proved to have all the eggs, larvae, and pupae in one spot.

During several periods of cold weather, workers of *dentata* were the only ants carrying on conspicuous above-ground activity. A point which further indicates its adaptability to adverse conditions is that *dentata* is one of the few ants which regularly forages in swamps during the periods of high water, when very little soil is above water, and all of the soil is saturated.

The feeding habits of this energetic *Pheidole* are diverse. It is attracted to a mixture of peanut butter and oatmeal used in mammal traps, to liver, and to molasses. These ants have been seen carrying collembola and termites. When a nest of *Reticulitermes flavipes* was opened, they were almost immediately on the scene, carrying termites away. As time passed, more ants entered into the activity. The termites were either paralyzed into stillness or killed, or were able to move only slightly while being carried. Most seemed fatally injured after they had been carried by an ant.

The following have been taken in the nests with *Ph. dentata*: Isoptera, various spp.; Corrodentia; *Orasema*, possibly *robertsoni* (det. A. B. Gahan, U. S. N. M.) (Gainesville) (Hym.); *Orasema robertsoni* Gahan (Hym.) (det. A. B. Gahan, U. S. N. M.).[4]

PHEIDOLE DENTIGULA M. R. Smith

Ph. dentigula is not a common ant on the Reserve although it was taken in 8 of the 15 stations. Its nests were found commonly to occasionally in mesic and hydric hammock; occasionally in scrub, Pomello scrubby flatwoods, Plummer slash pine flatwoods, xeric hammock, and bayhead; and a questionable record was made on the basis of workers alone from Rutledge slash pine flatwoods.

All except one nest, taken under litter, were found in the surface stratum. *Ph. dentigula* preferred nests in logs and in the bark at the bases of living trees, but it was also found in stumps, under litter, and one collection was made from fern roots. Nests in wood were almost equally divided between pine and broadleaved logs or stumps which ranged from moist to wet. Most of the nests were in soft or well-decayed wood, but many nests were backed by hard wood.

The number of individuals in the nests varied widely, although none was large. An average nest contained 85 workers and 17 soldiers (including callows), and 43 worker pupae and 7 soldier pupae. Most, but not all, of the nests had a queen. Immatures were present all year. Females were found on the wing in July and in the nests in September, and males were taken

[4] See Van Pelt (1950) for a discussion of *Orasema* in *Pheidole dentata* nests.

in nests in August. One nest contained only two workers, but had eggs and larvae.

Ph. dentigula is one of the species with which *Solenopsis molesta* has been found associated. In addition to the *Solenopsis*, *Paratrechina parvula* was taken with *Pheidole dentigula* from under litter.

PHEIDOLE FLORIDANA Emery

Smith has compared specimens of this ant with the original series in the U. S. National Museum. He says (corresp.) that although the Welaka specimens are "close to *floridana* they are not typical. *Floridana* has much more of the posterior part and side of the head, and thorax less heavily sculptured than your specimens. The postpetiole is also larger and less angulate on the side." The sculpturing and shape of the postpetiole have been found to vary to only a negligible degree on the Reserve. No specimens have been taken on the Reserve which approach individuals of *floridana* collected by the author in southern Florida. However, since both Gregg and Cole would assign these specimens to *Ph. floridana*, they are treated so here.

This *Pheidole* replaces *Monomorium pharaonis*, prevalent in the Gainesville region, in and around the houses of the Reserve. In non-ruderal areas it shows a preference for turkey oak and bluejack oak, where its nests occur commonly. Nests are also common in Pomello scrubby flatwoods. They are occasional to common in mesic hammock, and have been found rarely or occasionally in scrub, Leon scrubby flatwoods, longleaf pine flatwoods, Plummer and Rutledge slash pine flatwoods, black pine-fetterbush flatwoods, xeric and hydric hammocks, and river swamp.

Nests of this form have been found most often in the surface stratum, but almost as many have been taken in sand. It occupies a variety of nesting sites. In order of preference they are: 1) in dead stumps, 2) under litter, 3) in fallen logs, 4) under logs, 5) in litter, 6) in open sand (rudimentary craters, complete craters), 7) in and under logs, and 8) in bases of living trees. One collection was made from under the mat of a palmetto root.

Nests in sand have a cover of some sort. Although some nests had well-formed craters, all were covered with one or several leaves. The rudimentary craters were all found against the foundations of buildings, and it is possible that the ants here lived in crevices in cement or under pieces of cement. Those nests in wood were usually in wet logs or stumps, and although nests occurred in wood in all stages of decay, more were in the later stages. Many collections were made under bark, and neither broad-leaved nor pine wood was preferred.

Nests of this form are not populous, and seem to be smaller than *Ph. dentigula*. A nest, perhaps slightly smaller than average, contained 35 workers and 6 soldiers along with immatures. Immatures probably occur all year, and winged forms are present during the summer months. In some nests in wood it is difficult to delimit the boundaries of the colony. Individuals in these cases are found throughout the log, and there is no single, compact nest group.

This moderately active *Pheidole* is attracted to grease in kitchens. On

several occasions it was taken eating the peanut butter and oatmeal bait of mammal traps, and in other instances it was found between the septa of large mushrooms. Mr. J. C. Moore found this ant on the Reserve in several fox squirrel nests. It continues its foraging activities into the night.

In one nest a beetle of the family Lathrididae was found associated with the ant in a stump in turkey oak.

PHEIDOLE METALLESCENS Emery

Ph. metallescens prefers the higher, drier areas. It occurs abundantly to commonly in turkey oak, Leon scrubby flatwoods, and xeric hammock; commonly in bluejack oak and scrub; occasionally in mesic hammock; and has been found only rarely in longleaf pine flatwoods, but may occur more abundantly there. It is often found in firelanes.

Approximately equal numbers of nests have been found in the subterranean stratum and in the surface stratum. Often, especially in turkey oak, nests have no crater, and the nest opening is entirely or partially covered by a single leaf. Some nests can be found in and around the root systems of herbs. The complete crater is characteristic of open ground, and in this situation incomplete craters can also be found. Nests of this latter kind vary in outside diameter of the crater from 2 to 3 inches, and in height from 1/8 to 1/2 inch; all of these nests have one opening. Many other nests occur in sand under leaf litter, and some of them maintain elementary craters.

The locations of nests in fallen logs vary from near or on hard wood to wood merging with substratum; either the bark may still be intact or it may be absent. The wood may be dry, or moist, or wet.

A nest taken from a log in scrub contained 505 workers and 29 soldiers with 1 queen. Immatures occur the whole year. No information concerning the time of appearance of winged forms was obtained. One nest, taken in the middle of January, 1950, from a firelane, contained large chambers of workers within six inches of the surface.

This fairly fast moving ant has a varied diet. It is attracted to liver and to molasses. Foraging activities extend into the night.

PHEIDOLE MORRISI Forel

Ph. morrisi is another of the ants which prefers the higher, more open areas of the Reserve. It occurs occasionally to commonly in turkey oak and xeric hammock, and occasionally in bluejack oak and Pomello and Leon scrubby flatwoods. Characteristically its nests appear along the dirt shoulders of roads, in firelanes, and in the areas around houses.

All of the nests of this species were in the subterranean stratum. Most of the nests were built in open sand, but some were constructed under leaf litter. Half of the nests had no crater, and the other half were built around a grass tuft or in lawn, where a rudimentary crater was thrown up beside the plants. Sometimes these craters were built beside a fallen log under which the colony could be found. Craters of *morrisi* built in the open were about 4 to 5 inches in diameter, and 1 1/2 to 2 inches in height. A majority of nests had only one opening, but there were several with two, and a few with three, openings.

An unusually large nest of *morrisi* contained 3500 workers and 350 soldiers. An average nest probably contains 1000 individuals. The immature forms are absent from the nests from late December to February. Winged forms have been taken in July.

Ph. morrisi is an active ant, and each colony employs numerous speedy workers for foraging. Foraging activities are carried on at night. It seems, however, to show a seasonal relationship in its aboveground activity. In the winter months foraging ceases almost altogether, and the ants remain in the nest, about three feet below the ground surface.

Molasses attracts *Ph. morrisi.* It has been seen to pick up eggs and larvae, and even workers of *Crematogaster ashmeadi,* but no interpretation of this activity is attempted here.

Solenopsis pergandei and *Paratrechina arenivaga,* as well as an unidentified species of Diptera, have been found in nests of *Ph. morrisi.*

PHEIDOLE PILIFERA (Roger)

This is not a typical form of *Ph. pilifera.* On the soldier, the transverse rugulae on the occipital lobes are finer and more indistinct than typical; the longitudinal sculpture is less dense; and the genae and dorsal occipital lobes are more shining. However, there is little reason to suspect at present that this variation is a new subspecies.

Even though there are open woods with some grass in them on the Reserve, this ant was found only in ruderal areas, namely in lawns and in orange groves. Here its occurrence was occasional. All nests were complete craters which varied in diameter from 3 to 4 inches, and in height from ¼ to ⅜ inches. All of the craters had only one nest opening.

Ph. pilifera, with its extremely large-headed workers, was recorded nesting with *Paratrechina arenivaga* and *Solenopsis pergandei.*

CARDIOCONDYLA EMERYI Forel

Foraging workers of *C. emeryi* were taken occasionally in xeric hammock and rarely in bluejack oak. Its nests in these situations have probably all been under litter, or perhaps in open sand. Smith (1944) states that these ants in Puerto Rico nest most commonly in sandy soil, but also in clay soil. Besides the above-mentioned stations, *emeryi* has been taken in the sand roads of the Reserve.

This small, slow-moving ant is attracted in great numbers to molasses traps. It continues its foraging activities into the night. Females were taken in flight in early December of 1949. Nests may be approximately the same size as those of *C. nuda minutior.*

CARDIOCONDYLA NUDA MINUTIOR Forel

On the basis of the few collections made of *C. nuda minutior,* firelanes and dirt roads, especially in high areas such as xeric hammock, seem to be its preferred nesting situations. On several occasions the grillwork of an automobile which had just passed through the high grass that grows in the

xeric hammock roads was covered with workers of this form. It was collected rarely in longleaf pine flatwoods, and it was found foraging along the edge of a bayhead where it abutted a sand road.

Like *Solenopsis globularia littoralis*, *C. nuda minutior* has been found only in unprotected palmetto roots. These nests are on the under side of the root, rather deep in the fine scalings of the wood.

The ant nests in small colonies of about 20 individuals. Females were taken on the wing in August, and female pupae were observed in the nest in the same month.

CARDIOCONDYLA WROUGHTONI BIMACULATA Wheeler

C. wroughtoni bimaculata has been collected commonly in turkey oak, and only rarely in Leon scrubby flatwoods and longleaf pine flatwoods. Since it is common in turkey oak, there is no apparent reason why it should not be found in other of the high areas such as xeric hammock. Numerous nests can be found abundantly in clumps of bamboo planted near the buildings of the Reserve.

In turkey oak, nests of this ant are found most often in stumps of longleaf pine (*Pinus palustris*) or turkey oak (*Quercus laevis*). All of these nests have been in or next to hard wood, with a little debris or softer wood near the nest. The species has also been taken from logs of longleaf pine, either dry or moist; from the moist base of an *Andropogon* stem; and from an oleander twig in which the nest was partly in the center of the stem, partly in the wood at the nodes, and partly under the thin bark in debris. It nests in a very similar way in and around the nodes of bamboo. Nests can thus be found in both the surface and herbaceous strata.

Of 3 nests taken in turkey oak and 1 in bamboo, that in the bamboo was the largest. These counted nests varied in number of workers from 21 to 43, and averaged about 32 workers. The number of queens increased with the size of the nest. The smallest nest contained 1 queen, while the others had 2, 4, and 5 queens respectively. All of the workers and queens were in one or two central chambers, and were not difficult to collect. Immature forms occur in all months. Females have been found in the nests in October, and a flight is recorded on October 7, 1949. What seemed to be an incipient nest without workers was observed in May, indicating that perhaps the females fly again in April or May, or that the workers are not hatched out during the winter.

This ant is moderately fast moving, and somewhat deliberate in its motions. Most of its foraging is done on days when the temperature is high (above 28° C) and the relative humidity is relatively low (below 40%).

CREMATOGASTER MINUTISSIMA MISSOURIENSIS Emery

Creighton (1950) lists the range of this ant from Texas to Missouri. *C. minutissima minutissima* is presented as replacing it from South Carolina to Florida and westward through the Gulf States to Texas. However, specimens from the Gainesville region and from Welaka have been consistently identified by Dr. M. R. Smith of the U. S. N. M. as *missouriensis*. These locality

records make it doubtful that *minutissima* and *missouriensis* are subspecies of *minutissima*. Until it can be proved, however, that they are variations of the same form, *missouriensis* will be recognized as a subspecies of *minutissima*.

During the course of the present investigation, it was found that *missouriensis* prefers the more hydric situations, although it has also been taken in the higher areas. It nested commonly in Plummer slash pine flatwoods, mesic hammock, hydric hammock, and bayhead, preferring hydric hammock; occasionally in bluejack oak, scrub, Rutledge slash pine flatwoods, and xeric hammock; and rarely in Pomello scrubby flatwoods and river swamp. In the Gainesville region, the ant was found in very similar situations.

C. minutissima missouriensis preferred nests on the soil surface, but many nests were found arboreally. Several nests were also taken in the subterranean stratum. The ant nested most often in fallen logs, bases of living trees, in small branches, in dead stumps, and under the mat of palmetto roots and trunks. It was also taken in the following places: under logs; in and under moss on a palmetto root; in a debris-filled and well-decayed *Pinus clausa* cone under litter; under the outer sheath of a dead flower stalk of *Serenoa repens;* under moss at the base of an oak tree. Nesting conditions varied from dry in small branches to wet in logs buried under litter. Other authors (Buren, 1944, and Cole, 1940) have found the majority of nests in sand under stones.

A colony from a small branch in hydric hammock contained 208 workers (including callows), 102 worker pupae, and 8 queens. This colony was a unit, but many colonies appear to occupy several different levels in a nesting place such as a log or the base of a living tree. A typical nest, arranged among debris-filled regions along 10 inches of a log, occupied cavities on the hard wood near the outside.

In a situation of this sort it is difficult, and perhaps really unnecessary for the present purposes, to be sure that one is dealing with only one colony. One may ask what is the criterion which will distinguish a section of a colony from a whole colony. The presence of supernumerary queens in some colonies of *missouriensis* makes it impossible to be sure one is dealing with a whole colony when one queen is observed. Likewise, here and in the subgenus *Acrocoelia,* if a queen is observed, there may be other, queenless parts of the colony in other places. Groups of workers have been observed in *Crematogaster,* especially in *Acrocoelia,* (and in other genera to some extent) with an abundance of immatures and no queen. Unless intercourse between a queenless group and a group with a queen is observed, it would not be clear whether the queenless group carries its eggs from a mother queen in another nesting place, or whether the workers are independent and lay their own eggs. In treating this situation throughout this study, each physically distinct aggregation is called a nest.

Cole (1940), in his report on the ants of the Great Smoky Mountains, mentions a nest of *missouriensis* with only 47 workers, but 56 supernumerary queens. On the Reserve, immatures in the nest are usually absent during periods of cold weather, but a few are present in most nests all year. Winged form pupae have been found in the nests in May, and winged forms have been taken through August. One instance of female pupae in October was

observed, and in January males were taken on one occasion wandering about during the day.

This is a slow to moderately fast moving ant. It is attracted to molasses traps.

CREMATOGASTER ASHMEADI Mayr

C. ashmeadi nests occur very commonly in all of the well drained areas of the Reserve, and occasionally in the hammock areas and river swamp. Except for their occasional to common occurrence in longleaf pine flatwoods, they are found only rarely in poorly drained flatwoods. *C. clara* Mayr tends strongly to replace *ashmeadi* in the flatwoods areas and in bayhead and marsh.

C. ashmeadi has been taken abundantly in Pomello scrubby flatwoods; commonly in scrub, Leon scrubby flatwoods, and longleaf pine flatwoods; occasionally to commonly in turkey oak, bluejack oak, and xeric hammock; occasionally in mesic hammock, and river swamp; and rarely in Plummer slash pine flatwoods, black pine-fetterbush flatwoods, and hydric hammock.

By far the majority of collections were made arboreally, but other nests were taken in the surface stratum. Most often, the ant was found in small branches. The other nesting sites in order of importance to the ant are as follows: twigs, galls, fallen logs, dead stumps, and one collection was made in the base of a living tree. Most of the nests in small branches were found in either scrub oaks or in *Pinus clausa*. Nests were also taken from the logs of fallen sand pine, usually from under bark on the top side. Although the ant seemed to prefer nesting sites in scrubby oaks, its presence in pine logs and branches indicates that its exclusion from poorly drained flatwoods is not due to an inability to live in pine.

The nests in twigs were on scrubby oaks, or else in grape vines. Those in scrubby oak galls were usually in pendent, spherical galls. Some were in other, variously shaped galls, especially the type around stems; in these the ant occupied the several different compartments from which the gall wasps had emerged. Nests were in either broadleaved or pine logs or stumps, but were in all cases dry or moist. This preference for dry or moist conditions in nesting sites supports the contention that this ant prefers the drier situations.

In the Gainesville region, drier situations, among them ruderal areas, were also preferred. In the same manner Cole (1940) has found *ashmeadi* nesting in dry situations.

In the discussion of the life history of *C. minutissima missouriensis*, it was brought out that on many occasions what may seem to be a colony of *Acrocoelia* may be merely a section of a larger aggregate, the true colony. It was pointed out that each of these sections is here recognized as a nest.

The number of workers contained in 18 nests ranged from 4 to 425, averaging 137. In none of these nests was a queen found. These nests had an average of 23 callow workers. The nest with the largest number of workers, taken in a small branch in Pomello scrubby flatwoods, contained 51 females and 11 males, while another nest of 185 workers contained no females and 38 males. Of those that contained winged forms, 12 were sex specific, while the others contained at least three times as many individuals of one sex as of the other. The largest nest contained 220 worker pupae,

whereas the other nests averaged about 25 worker pupae. Winged forms were found in the nests in July through December. Single males have been taken in January.

In times of excitement, *C. ashmeadi* extends its heart-shaped gaster above its head and runs quickly over the ground or the vegetation. Under normal circumstances, this is a slow to moderately fast moving ant. Many times when a nest is opened during a cold period when the nest is inactive, the workers do not move, but lie with their bodies pressed flat against the surface to which they are clinging. Such is also true of the other members of the subgenus.

In September, 1948, collections in Pomello scrubby flatwoods showed a remarkable abundance of *C. ashmeadi,* especially in galls, and in small branches. This large population was within a circumscribed area of the station, and may have been coincidental with the galls and the small branches becoming suitable for the ants. A seasonal high was also noticed in Leon scrubby flatwoods in December. During 1949 no such high was observed in either station.

Although this subgenus is noted for attending honeydew-secreting insects, they have been observed carrying various kinds of dead insects into their nests. On one occasion an aggregate of *C. ashmeadi* was noted in a crotch of a saw palmetto (*Serenoa repens*) frond; workers were carrying away parts of a dead grasshopper nymph. The workers have repeatedly ventured into the cyanide jar of a light trap in order to carry away insects. They have also been found, probably as casuals, in fox squirrel nests by Mr. J. C. Moore.

Nests have been observed adjacent to those of the termites *Kalotermes* (*jouteli*?) In one nest containing winged forms, a dipteran, resembling quite closely the males of *ashmeadi,* was found.

Some of the workers found on the Reserve have a somewhat opaque and slightly punctate thorax, differing from the usual shiny, smooth thorax. One colony, the only one taken from under the bark of a living tree (*Pinus palustris*), contained workers with a lighter appearance than usual. The head and thorax are light brown, while the gaster is dark. The queen is all light brown, and measures 1.8 mm along the dorsum of the alinotum; other queens of *C. ashmeadi* measure 2.0 mm along the dorsum, and are all dark brown or black.

CREMATOGASTER COARCTATA VERMICULATA Emery[5]

The specimens listed here were assigned to *Crematogaster vermiculata* by M. R. Smith. The collections of this ant, which has its type locality in Los Angeles, are the first Florida records.

Nests of this subspecies have been confined to two stations. *C. coarctata vermiculata* was collected occasionally in hydric hammock and river swamp. In all cases it was nesting arboreally, in most cases in twigs of sweetgum (*Liquidambar styraciflua*) or some one of the bay trees. Such twigs may have

[5] Buren (corresp.) feels that this form is cospecific with the *vermiculata* of Emery (1895), but that it does not correspond with *coarctata vermiculata* of Creighton (1950); this last form is "probably cospecific with *californica* Emery, 1895."

a half dozen openings to accommodate a colony. On one occasion it was found nesting in the crotch along the midrib of a *Sabal palmetto* frond under the debris gathered there. Other ants, especially *Crematogaster ashmeadi* and *Paratrechina parvula*, are also found nesting on palmetto fronds.

The distribution of *vermiculata* in stations and nesting sites on the Reserve indicates rather strongly that it will always be found in moist or hydric situations, and probably always above ground. In Gainesville, this form was taken in scrubby flatwoods, in an area where the plant association offered mesic conditions.

It is possible that the nests of this ant extend into two or more twigs. If this is the case, each twig of such a colony contains only a section of the whole colony, but each of these sections, as explained before, is treated as a nest here. One very long twig contained a whole colony. A count of this colony yielded 1085 workers, 162 worker callows, 7 reproductive and 710 worker pupae, 25 reproductive and 221 worker larvae, and numerous eggs. The presence of reproductive pupae and larvae in the nest, taken in July, indicates that winged forms would soon be present. Winged forms were taken in another nest in October.

The habits of *vermiculata* are much like those of *ashmeadi*.

CREMATOGASTER CLARA Mayr

The original determinations of the ants listed under this heading were made by M. R. Smith as *C. laeviuscula*. An indication of a dispute over the naming of these insects was furnished by Creighton (1950) when he cited the range of *laeviuscula* as "Oklahoma southwestward through Texas . . . .". Recent correspondence with Buren has introduced a new aspect. Buren feels that *clara* Mayr, synonymized by Creighton under *laeviuscula*, is a distinct species; and that the specimens from the Reserve are either *clara* or *atkinsoni* Wheeler on the basis of distribution. Upon subsequent determination, Smith felt that some of the group originally called *laeviuscula* on the Reserve were in fact *clara;* others he would determine no farther than genus. These last specimens have in large part come from carton nests in a *Spartina* marsh.

In 1949, Creighton identified carton nest specimens from a *Spartina* marsh at Cedar Keys, Florida, 65 miles to the west of Welaka, as similar to *atkinsoni*. These specimens differed from the typical *atkinsoni* in having less thoracic pilosity. It is therefore possible that we have in this section of Florida a complex which is closer to the typical *atkinsoni* than to any other known form, or which is actually an extreme variation of *atkinsoni* itself.

Until positive determinations can be made in this intricate group, the trivial name of *clara* will be used to designate all the forms originally listed as *laeviuscula*. Attention should be brought to the fact that *clara*, as used here, possibly includes closely related forms, such as *atkinsoni*.

C. clara prefers to nest in the poorly drained flatwoods areas of the Reserve, and in the wetter areas of hammock and seasonally flooded plant associations. In this way it tends to replace *C. ashmeadi*, although there are areas of overlap in the distribution of the two species, especially in longleaf pine flatwoods, and in mesic hammock.

C. clara was found abundantly in Rutledge slash pine flatwoods and in marsh; commonly in longleaf pine flatwoods, Plummer slash pine flatwoods, hydric hammock, and bayhead; occasionally in bluejack oak and mesic hammock; and rarely in turkey oak and xeric hammock. Its absence from black pine-fetterbush flatwoods may be due to the scarcity of logs in that station, but it may also depend on the relative openness and consequent high rate of evaporation and prolonged periods of dryness of the area.

Nests of *clara* were found in all strata except the subterranean; most were arboreal; and a few were in the herbaceous stratum. Small branches and fallen logs are the most preferred nesting sites. *C. clara,* however, uses small branches less than half as many times as *ashmeadi,* whereas it nests in fallen logs much more often than *ashmeadi.* In order of preference other nesting sites in which *clara* has been found are: twigs, dead stumps, carton, sawgrass flower stems. Single collections have been made from an *Andropogon* stem, a dried leaf of *Sagittaria* between septa, a flower stalk of *Sabal palmetto* on ground, and from under pine needle litter on saw palmetto frond two feet above ground.

In a majority of the cases, the nests in logs were in or against hard wood, but some nests were in softer wood. Nests were in logs of all stages of decay, from those merging with the soil to those in which the wood was in the first stage of decay. Some nests were under the bark of fallen logs. Nests of carton were observed on occasion in the sawgrass (*Mariscus jamaicensis*) marsh, but always on a flower stalk of sawgrass; in these cases the nests occupied both the carton and the flower stalk. Never was the carton portion of such a nest far above the water surface.

In the marsh grass (*Spartina bakeri*) marsh on Buzzard's Roost, carton nests were abundant. Except for a few *clara* in twigs, no other nesting site was observed to be occupied by ants in this marsh. Nests are usually one or two feet above the base of the *Spartina* clump, shaded by the tops of the grass blades. Each nest in marsh grass binds together a number of grass blades, usually the middle dozen or so of each grass clump, and is held up by them. Nests are quite large, measuring, on the average, 12 inches vertically and 4 inches horizontally. One nest measured 20 inches vertically and 6 inches horizontally. They are constructed of plant material, usually bits of leaves, together with large sections or whole leaves of maple or wax myrtle curled around the supporting grass. The nests are quite moist on the inside, but are always dry on the outside. Several nests, built in the crotches of shrubs, extended from the carton into the adjoining hollow stems.

Nests of *C. clara* are numerically about the same size as those of *C. ashmeadi.* The range of numbers of workers in the 7 nests counted was from 16 to 300, averaging 128. None of these nests contained queens. Nests and sections of nests are considered synonymous here in the manner discussed under *C. ashmeadi.* The cold spells on the Reserve seem to be coincidental with the absence of immature forms in the nests. Reproductive pupae appear in the nests in April, and winged forms have been taken in June through July, and again in October through December. Only 2 out of the 10 nests from which winged forms were taken, contained both males and females.

On June 27, 1948, a nest was observed in Rutledge slash pine flatwoods from which excited workers were emerging and hastily running along the low

shrubs surrounding the twig nesting site. Along with the excited workers were males, evidently ready to make a flight, although no male was seen to fly. A nest brought into the laboratory on November 26, 1949 contained males which immediately attempted to wander from the nest, although no flight was observed. The males and attendant workers aggregated under the bucket in which the carton nest had been placed. Perhaps this restlessness was preflight activity, or was merely due to overexposure of the nest to sun with a consequent change in temperature and relative humidity in the nest. (It is possible that in nature a sharp enough change in the physical conditions of the nest can evoke flight.) The next day the nest was placed over water in an attempt to keep the ants in their nest. On November 29, the males were noted investigating the ends of the cut marsh grass, but no flight took place. Because of their restlessness, a large number of males had fallen into the water and drowned by the next day, and observations were discontinued.

The habits of movement and feeding are much like those discussed under *C. ashmeadi*. Dead insects have been found in nests of *C. clara*, and the ant is attracted to molasses traps. On one occasion workers seemingly were attending scale insects on a palm frond. Nests have been noted near nests of termites, the workers of each freely intermingling. They were seen to stroke the termites with their antennae and palpi on all parts of the termite's body, but mainly in the head and thorax regions. Small mites have been found on the antennae of several workers. The size of many individuals in marsh is strikingly larger than that of those in other plant associations. Total body length ranged in one nest from 3.0 to 4.8 mm, whereas workers from other stations range from 2.5 mm to 3.3 mm in total body length.

CREMATOGASTER LINEOLATA (Say)

Creighton (1950) notes that *C. lineolata* is found the farthest south in the Appalachian Highlands of northern Georgia, and that an altitudinal difference separates *lineolata* from the subspecies *subopaca*. *C. lineolata* is reported to have its range at low to moderate elevations in the South Atlantic States, as well as to the west and north.

Specimens which are labelled *C. lineolata*, sent to the author by Dr. Smith, key out to *C. lineolata subopaca* in Creighton's key. On the other hand, those specimens which were taken on the Reserve can be assigned to *lineolata* on the basis of his key. According to the distribution Creighton cites, *subopaca*, and not *lineolata*, should occur here. Since it will not be clear what name should be assigned to this ant until a thorough revisionary study has been made, the name *lineolata* will be used here in the broad sense.

C. lineolata was taken in only three stations. It occurs commonly in Pomello scrubby flatwoods, and occasionally in Leon scrubby flatwoods and xeric hammock. Nests have been found in almost equal abundance in the surface stratum and in the subterranean stratum under litter.

Its nesting sites have been approximately evenly divided between nests under litter, in litter, in fallen logs, in dead stumps, and in small branches. The nests in logs and stumps were in oak for the most part, but some were found in pine. The relatively few nests in pine sets *lineolata* apart from the

other members of the subgenus on the Reserve, but the difference may be due to the distribution of the species in stations where the main trees forming logs and stumps are oak rather than pine. In this respect it can be noted that *lineolata* follows the distribution trend of *ashmeadi* rather than that of *clara,* occurring in the better drained areas of the Reserve. Cole (1940) indicates, as do the above observations, that this species lives as often in the soil as in wood. He mentions that nests under stones loosely resting on the soil are a favorable nesting site.

One nest from Pomello scrubby flatwoods contained 184 workers, 3 callow workers, and 35 worker pupae. No queen was taken. Cold weather, as it does with the other species of the subgenus on the Reserve, seems to inhibit the production of eggs. Pupae of males and females were seen in nests at the end of March, and males were taken in the nest in May. No information concerning winged females was obtained.

C. lineolata has much the same habits as the others of the subgenus on the Reserve. It is a moderately fast moving ant. Because of its distribution on the Reserve, it was taken in most cases when the temperatures were high and the relative humidity low. It was observed attending aphids, and probably also uses insects as food.

MONOMORIUM FLORICOLA (Jerdon)

One specimen of this species was collected wandering on a sawdust pile in turkey oak. This introduced species is well distributed over Central America and the West Indies. Wheeler (1908), writing of the ants of Puerto Rico and the Virgin Islands, states that these ants are "Common in Tillandsias, under bark-scales of trees and in hollow twigs. All the females were apterous . . . ."

MONOMORIUM MINIMUM (Buckley)

M. minimum was taken occasionally in only one station, namely turkey oak. It was, however, found also in firelanes, and was one of the more common occupants of the latter areas. In most cases this ant nested in craters, either incomplete or complete, but some nests were found under very light litter. The craters, all with one nest opening, varied in diameter from 2½ to 4 inches, and in height from ½ to 1¾ inches.

In the Gainesville region, *minimum* was usually found nesting in logs, or under logs or other cover. It seems to be well distributed throughout the United States.

During the work of bringing pellets of sand to the surface, this moderately fast moving, diligent ant employs many workers, and thereby gives the nest the appearance of bustling activity. By comparing a vial filled with a known number of ants and another filled with an unknown number, a total of about 3000 workers was estimated for one nest. Several termites were taken with this colony.

SOLENOPSIS GEMINATA (Fabricius)

The close morphological resemblance of this ant and *S. geminata rufa* is discussed under the latter ant. Since the lack of the mesosternal spine

in this form seems to be an untrustworthy character to differentiate it from *rufa,* the darker color of *geminata* has been used here to distinguish the two forms.

S. geminata was found in nine stations, but it was taken commonly only in Leon scrubby flatwoods. Occasional collections were made from turkey oak, bluejack oak, Pomello scrubby flatwoods, longleaf pine flatwoods, xeric hammock, hydric hammock, and river swamp; and one nest was found in scrub. Firelanes also offered a favorable nesting site. In the Gainesville region it was found more commonly, and was also taken in mesic hammock.

On the Reserve, *geminata* has for the most part occupied the subterranean stratum, but has also been found in the surface stratum. Most of its nests are asymmetrical, rudimentary craters, or are in sand under litter. Other nests were found in incomplete craters, complete craters, in a palmetto root on the ground, and under a longleaf pine log. This last colony had produced a crater at the side of the log.

The nests with incomplete and complete craters were very likely incipient nests, or nests with small numbers of individuals. As these nests grow in size, the several grouped craters fuse to form a large, rudimentary crater. Many of the rudimentary craters, on the other hand, are begun around a clump of grass which soon becomes buried under the sand of the crater. Some rudimentary craters are built in the form of a string of craters, sometimes up to eight feet in length. One rudimentary crater was begun around the base of a scrub oak, and was composed of sand, leaves, and small pieces of rootlets. Rudimentary craters have been observed ranging from 4 inches to over 1½ feet in diameter; from 1 inch to almost ½ foot in height; and in number of nest openings from 1 to 20 or more.

This "fire ant" is moderately agile, much like *rufa.* It has been attracted to mammal traps baited with peanut butter and oatmeal. Small seeds, such as alyceclover and carpetgrass, make up part of its food, but the ant's small size makes larger seeds too difficult to carry. The workers also derive honeydew from aphids on the roots of plants near their nest.

Winged forms have been observed in June and July. Immatures appear most numerous in the summer.

SOLENOPSIS GEMINATA RUFA (Jerdon)

This form has been listed by Creighton (1950) and previous authors as *S. geminata rufa.* Creighton, however, points out that the characters used to separate *geminata* from *rufa* may have been given more prominence than they deserve, and that the character of the mesosternal spine in *rufa* is more valid for the Asiatic specimens than for those from the United States. In America *rufa* and *geminata* are found in practically the same areas, making it impossible to treat *rufa* as a geographical subspecies. On the other hand *rufa* and *geminata* are found to intergrade, making it difficult to treat them as separate species. Creighton states: "In this country *rufa* behaves as a color variety and shows no geographical distinctions. I have retained it as a subspecies because this behavior may be a result of introduction." Evidently there is material which has come to Creighton's attention that

makes him believe that *rufa* and *geminata* are not synonymous. Doubt still exists as to the taxonomic status of *rufa*.

Specimens of *rufa* were found rarely in turkey oak and longleaf pine flatwoods, and occasionally in Plummer slash pine flatwoods. Colonies have been taken from both the surface and subterranean strata. Nests are found most often with rudimentary craters or under litter in sand. One nest was found in the under side of a turkey oak (*Quercus laevis*) log. Part of this last colony was in the log and a lesser part in the sand under the log. The rudimentary craters or mounds may reach a diameter of 2 feet and a height of 1 foot, with numerous nest openings. To build these nests *S. rufa* seeks the more open areas. For example, the nest in longleaf pine flatwoods was partly in the flatwoods proper and partly in a firelane which was cut through the flatwoods. *S. rufa* has also been taken nesting in ruderal bamboo.

In the Gainesville region the hammocks provided nesting sites for this ant. Its abundance around Gainesville was higher than on the Reserve, probably because of the more open nature of the ground. There is also the possibility that, because it is a "tramp" form, it has spread more widely in the residential districts and their surrounding areas, than in the more natural area of the Reserve. In the Gainesville region, small craters were often seen built around grass clumps. As the nest grew and more sand was brought to the surface, the grass was buried.

S. geminata rufa is a moderately fast moving ant. Sweeping with an insect net across low vegetation has, on several occasions, yielded specimens of this form. Flights of winged forms have been observed in May and October.

SOLENOPSIS GLOBULARIA LITTORALIS Creighton

S. globularia littoralis is one of the few ants collected more than once which occur in only one plant association of the Reserve. It was found occasionally in black pine-fetterbush flatwoods. In Gainesville, the ant was confined to the open, almost scrubless flatwoods which are commonly used as pastureland in that area.

The nests on the Reserve were found to be only in the surface stratum. Typical nests were in palmetto roots thrown up on the soil surface. In the palmetto root the nest was built between the overlapping flakes of the bases of fronds, and was on the under side near the soil. One nest was found in a grass clump, part of the nest being in the roots of the plant where the queen was located, and the rest being in the lower stems. In Gainesville, the ants were taken from under the bark of newly cut pine logs, and from nests built in sand and covered by small shavings of wood and pine needles.

One nest, taken in the black pine-fetterbush association of the Reserve, contained 46 workers and 1 queen, along with immature forms. No information as to when the sexual forms appear in the nests was obtained.

S. globularia littoralis is a moderately fast moving ant. It extends its above-ground activities into the night.

SOLENOPSIS MINUTISSIMA Emery?

The taxonomy of this small, insignificant ant has been one of the most confused of the ants of the Reserve. Smith (communication) says specimens

"agree very well with specimens collected in Haiti and recorded by Wheeler and Mann . . . . as *pollux* Forel . . . . Please do not consider the determination final as your specimens have not been checked with types or with the original description." The same specimens were sent to Creighton, who was cognizant of Smith's determination. He wrote that in his opinion the specimens were *minutissima* Emery. He says (communication): "Although I have not been able to compare your specimens with type material of *minutissima*, they agree so perfectly with Emery's figure and description of that species that there is little room for doubt on this point. The head of *minutissima* is more elongate than that of *pollux* and is narrowed behind. There are several other differences which distinguish the two species. Your specimens agree on every count with *minutissima* rather than with *pollux* . . . . *S. minutissima* was originally described from material taken in Buenos Aires, Argentina. The species would, therefore, be much more likely to establish itself in northern Florida than would a strictly tropical form." In another letter Creighton indicates that there is some doubt in his mind as to whether *minutissima* should have been synonymized with *laeviceps*. He says specimens from the Reserve may possibly be *laeviceps*, but he thinks it very likely that they are *minutissima*. From still another aspect, Brown, from a comparison of worker types, believes that *minutissima* and Smith's *longiceps* are synonymous.

This ant seems to prefer the mesic and hydric areas of the Reserve, although it has been taken in the better drained stations. Nests were occasional in turkey oak, bluejack oak, scrub, Pomello scrubby flatwoods, Plummer slash pine flatwoods, mesic hammock, hydric hammock, and bayhead; and rare in xeric hammock and river swamp.

All nests occurred in the surface stratum, mostly in the bases of living trees. The trees most preferred were slash pine (*Pinus elliotti*), probably because of the high relative humidity and low rate of evaporation usually around them. The ant was found also in longleaf pine (*Pinus palustris*) in xeric hammock and bluejack oak, and once in water oak (*Quercus nigra*). All of these nests were at the base of the tree in the bark below the soil or litter surface; all were wet, and usually contained some debris. These nests were in "sections" as discussed under *Crematogaster minutissima missouriensis*. Other nests were found in fallen logs and under the mat of palmetto root.

A count of 3 nests yielded a range in the number of workers from 22 to 39, averaging 29. These numbers are, in all likelihood, smaller than is characteristic of an average nest or section. Immatures were present in the nest in all parts of the year. What are believed to be reproductive form larvae were found in the nest in April. No further information concerning the winged forms was obtained.

The movements of this ant are even slower than those of *S. molesta*. Whenever a nest was broken into, the workers always remained motionless for a few seconds, perhaps long enough for the student to overlook them. As in the case of the Ponerine ants, which blend with their nesting sites, these ants are many times given away by the presence of their white immatures.

SOLENOPSIS MOLESTA (Say)

Certain of the specimens included under this heading differ somewhat from

the measurements given by Smith (1942) and Hayes (1920). These specimens are proportionately smaller than those described by these authors; they are also smaller than other specimens determined as *molesta* taken from the Reserve. Smith lists the worker length of *molesta* as 1.8 mm; Hayes gives the length of the worker as 1.5 mm to 1.8 mm. This last measurement is much closer to that of the range found on the Reserve, where workers varied from 1.45 to 1.8 mm. If these specimens all represent the same species, it is possible that the difference in length can be attributed to differences in the technique of measurement, but it would be evident that *molesta* workers have a wide range in total length, considering the size of the ant.

S. molesta finds its most preferred nesting sites in mesic or somewhat hydric stations. It was taken abundantly in mesic hammock; commonly in scrub, Plummer slash pine flatwoods, and hydric hammock; occasionally to commonly in Pomello scrubby flatwoods, longleaf pine flatwoods, and bayhead; occasionally in turkey oak, bluejack oak, Leon scrubby flatwoods, Rutledge slash pine flatwoods, black pine-fetterbush flatwoods, and xeric hammock. It is possible that it will also occur in marsh and swamp.

Nesting sites of *molesta* are preponderantly in the surface stratum of the Reserve. Only one nest was found in sand. In the Gainesville region, however, approximately half the nests were constructed in sand, either in the open around grass clumps, or under some sort of cover. Cole (1940) mentions only nests in sand for *molesta* in the Great Smoky Mountains: "The independent nests consisted of a very few tiny chambers and galleries lying very near the soil surface just beneath the cover of stone or wood." In seeming contradiction to the observations on the Reserve, Cole found *molesta* nests only in dry grassy areas. It is likely, however, that the ant makes use of the nesting places available in those areas in which it finds itself. Where there are no logs in the right stage of decomposition, it lives under stones or other material, and where there are favorable nesting sites in wood, it makes use of them.

In order of importance to the ant, the nesting sites in which *molesta* has been found on the Reserve are as follows: bases of living trees, under mat of palmetto root, in dead stump, in fallen log, in palmetto root on ground, in and under litter. It has also been found in the base of a grass clump, under sphagnum at base of live oak, and under sphagnum on saw palmetto root. Cases of lestobiosis have also been observed.

The majority of *S. molesta* nests in wood on the Reserve were in soft, wet wood which was decayed to fine debris. Those nests in saw palmetto roots were usually between the root and the bases of sloughed-off fronds where there was quite a bit of debris; as a rule, moss covered the roots. Nests in the bases of living trees were all in the bark below the soil surface, in a position where there was a great deal of moisture. Nests in fallen logs and stumps were found equally in pine and broadleaved (especially oak) wood.

Of the three nests counted, the number of workers ranged from 60 to 100, averaging 78. None of these had a queen. Nests which seemed to have at least 200 individuals have been seen. *S. molesta* seems to nest in "sections" as discussed under *Crematogaster minutissima missouriensis*. It offers some-

what the same problem as *missouriensis*, since it is small in size, and on many occasions can be found in the bases of living trees, especially pine, where sections of a nest in the bark may range almost the whole distance around the circumference. Hayes (1920), writing on the queen of *S. molesta* says: "It is an unusual thing to find a queen in out-door nests, and the number of queens in a colony, when found, vary from one to many. In a single instance 26 fertile, or at least wingless queens were taken in a colony containing a large number of workers and immature forms." In an attempt to explain the absence of queens from nests in the field, Hayes states further that "The life of a queen under artificial conditions is very short. None were able to live for an entire summer, or even be carried over the winter . . . . [but] Queens were found early in May in outdoor nests, indicating that they will live over an entire winter at least." Hayes makes no mention of the point that his nests may be only sections of complete colonies, and consequently have no queen. It is certain, however, that queens of *S. molesta* are not as easily obtainable as queens of certain other species.

The workers of this ant are small and move slowly, and, with their pale color, are difficult to see against light backgrounds. Winged forms have been observed in the nests in July and August, and immatures are present in every month.

Following is a list of the ants with which *S. molesta* has been found nesting: *Paratrechina arenivaga*, with *Solenopsis pergandei; Crematogaster ashmeadi; Aphaenogaster fulva; Pheidole dentigula.*

On February 22, 1947, in the Gainesville region, a nest taken from around a grass clump in turkey oak, in which the ants were perhaps attending aphids, contained a nymph of the family Miridae (Hemiptera) (det. R. I. Sailor, U. S. N. M.)

SOLENOPSIS PERGANDEI Forel

S. pergandei is the least common of the ants of the subgenus *Diplorhoptrum* on the Reserve. It was taken occasionally in turkey oak and xeric hammock, and rarely in Leon scrubby flatwoods and mesic hammock. This distribution indicates a preference for the better drained areas of the Reserve.

Most of the nests of *S. pergandei* were taken in the subterranean stratum, but the ant was also found in the surface stratum. It was found most often in nests of other ants. Other nests were taken under litter, under reindeer moss, and under the bark and in the wood of wet, fairly soft laurel oak logs. Nests of this ant in the Gainesville region were more numerous than in Welaka, and were built around small plants, clumps of grass, and one was found around the base of a mushroom. Those rudimentary nests all contained four or five openings.

S. pergandei, as mentioned above, has been noted to exhibit lestobiosis in nests of *Paratrechina arenivaga* and *Pheidole morrisi*. Groups of the *Solenopsis* were found about a foot below the soil surface in the dirt of these nests. In several instances, *S. molesta* was taken along with *pergandei* in *Paratrechina* nests.

S. pergandei is slow moving, and pale in color. These attributes make it difficult to detect, since it lives on pale colored sand in most cases. Females of this species have been taken in August.

SOLENOPSIS PICTA Emery

The distribution of *S. picta* in the Welaka Reserve is peculiar in that it occurs in 14 of the 15 stations worked, but in none does it occur with a high degree of relative abundance. It was found occasionally to commonly in bayhead; occasionally in all other stations except black pine-fetterbush flatwoods, xeric hammock, river swamp, and marsh. It was absent in marsh, and occurred rarely in the other three stations. Its distribution is more closely allied with the arboreal stratum than with any station or group of stations.

The greatest number of collections were made in the arboreal stratum, but several were also made in the surface stratum. The most common nesting sites, in order of preference, are as follows: small branches, twigs, galls, and fallen logs. The ants were also found under the mat of a palmetto root and in the base of a living tree, and what may have been a nest was recorded from under litter. Although more collections were made of nests in wood of broad-leaved trees, many collections were also made in pine, and the margin is not enough to indicate a preference.

Nests of *S. picta* are at times constructed in such a way that they might be interpreted as being "sections" as discussed under *Crematogaster minutissima missouriensis*. One such nest in a small branch contained 13 workers and no queen, while another in a gall contained 10 workers and no queen. In the case of the latter nest, it is possible that the rest of the colony was in a nearby gall which contained a queen with 48 workers. All other nests counted contained one queen each. In two small nests, there were 7 and 8 workers, respectively from a grass stem and from a shrub twig. One nest from a twig in mesic hammock contained 215 workers, while another from a twig in scrub contained 555 workers. Winged forms have been taken in July.

S. picta is rather slow in its movements. It has been taken nesting very close to *Paratrechina parvula* in a saw palmetto root, perhaps giving an example of lestobiosis. The *Solenopsis* has also been taken with termites. Mr. J. C. Moore, working on the fox squirrels of the Reserve, has found it in the mammal nests. He records that one such fox squirrel nest in which ants were found was 90% Spanish moss and well-soaked by frequent rains at the time of the collection. He states (communication) that "Certain beetles, lepidoptera, and stratiomyid fly larvae were much more abundant than the ants in the rotting interior."

MYRMECINA AMERICANA Emery

Only one specimen of this ant, from leaf litter in scrub, was taken during the study. Further search failed to discover the nesting site.

Gregg (1944) has found *americana* rare in the Chicago region and Buren (1944) lists it from Iowa. Cole (1940) sums up its habits in the Great Smoky Mountains in the following sentences:

> It has been found only in very moist habitats, where it lives in small colonies and constructs little nests in wet rotted hollow twigs, under dense masses of moss on logs on stones and beneath small stones. It was found to be a rather common representative of the meager ant fauna of the buckeye-basswood forest. Many of the colonies consisted of only 12 to 20 workers. The nests are of a very superficial nature and the chambers are generally those natural crevices which may be accessible. The workers are extremely slow of movement.

LEPTOTHORAX PERGANDEI FLORIDANUS Emery

L. pergandei floridanus occupied eleven stations. Although it prefers the higher, drier plant associations, it was taken several times in low flatwoods and low hammocks. Nests were, however, found to be excluded from the seasonally flooded areas. It is interesting to note that the subspecies has been collected most commonly in the low black pine-fetterbush flatwoods. Portions of this area occasionally contain standing water for a day or so at a time during the period of the hard summer rains. The ground, however, soon becomes dry, and the open terrain affords a habitat similar to a higher area. The other stations in which *floridanus* occurs commonly are turkey oak, bluejack oak, and Leon scrubby flatwoods. Nests were found occasionally to commonly in scrub, longleaf pine flatwoods, and xeric hammock; occasionally in Pomello scrubby flatwoods and mesic hammock; and rarely in Plummer slash pine flatwoods and hydric hammock.

Colonies were found, for the most part, in the surface stratum. Perhaps half as many nests were found in sand, but a majority of these were associated with wood such as the root system of living and dead fetterbush in the *P. serotina-Desmothamnus* association. One nest was taken from an *Andropogon* stem in the herbaceous stratum, and two colonies were collected from the arboreal stratum.

L. pergandei floridanus was collected most often from logs. In order of preference, other places from which nests have been collected are: 1) under leaf litter, 2) in dead stumps, 3) under mat on palmetto roots and trunks, 4) under and in logs, 5) in small branches, 6) in palmetto root, 7) in base of living tree, 8) in grass clump, 9) in *Andropogon* stem; 10) in rotting pine cone and 11) inside stem of rotting palmetto frond. Nests in debris were common, athough some contained a minimum of debris.

Of five colonies collected from the surface stratum and counted, the number of workers varied from 21 to 58, and averaged 36. Another nest was taken from a small branch and contained 2 callows and 111 workers. Each of these nests contained one queen. Still another nest was taken from a fallen log which contained only 18 workers and no queen; but perhaps this was only a section of the whole colony. Eggs, larvae, and pupae were found in all months, although not in all nests. Winged forms begin to appear in the nests in May and are absent again by August.

Usually this ant can be seen in moderate above-ground activity in all months of the year. Its mannerisms and appearance in the field are much like those of *Pheidole dentata*, and it is sometimes necessary to examine closely a wandering individual before a determination can be made.

LEPTOTHORAX TEXANUS DAVISI Wheeler

The collection of this ant in Florida extends the known range considerably, since the subspecies was known previously only from New Jersey and New York. Dr. M. R. Smith writes that the Florida specimens do not differ from the specimens collected in these northern localities.

L. texanus davisi was found occasionally in turkey oak and Leon scrubby

flatwoods, and rarely in bluejack oak, black pine-fetterbush flatwoods, and xeric hammock. It thus shows a preference for the higher, drier areas.

Its nesting sites have all been in the subterranean stratum, either under litter or with little or no crater in the open sand. One nest was discovered which had no apparent opening to the surface; the entire nest was within 1/4 inch of the surface.

A nest collected in turkey oak contained 18 workers and a queen, but no immature forms. No further information was obtained concerning the life history of this ant.

It is shy, and moves only moderately fast over the sand while foraging. Like *L. pergandei floridanus*, it moves about in somewhat the same manner as the much more common ant *Pheidole dentata*. It has been taken foraging with *Solenopsis geminata*, and a lone queen of *Camponotus socius* was taken with a *davisi* colony.

TETRAMORIUM GUINEENSE (F.)

This introduced species was found in four plant associations. However, only the single collection in turkey oak was taken from a station. Since the other collections were not made in stations, the relative abundance must be based solely on the few collecting trips made to the areas in question. These three remaining plant associations in which the ant was observed are similar to the descriptions of the nearby stations (Van Pelt, 1956). They all had in common their distribution along the St. Johns River, a fact which seems to support the idea that the form is introduced. Map 3 shows Buzzard's Roost in the southwest corner of the Reserve where the ant was taken rarely in river swamp and occasionally in hydric hammock. At Mud Springs, near the swamp station, the ant was taken occasionally in marsh. There is a possibility that it had only recently been introduced into turkey oak.

T. guineense was represented in the surface and the herbaceous strata. Here the herbaceous strata is extended to include the flower stalks of sawgrass. These vertical stalks, which become hollow inside with a usual bore of 1/4 to 3/8 inch, cannot be considered true twigs because of the large diameter of the bore, and because ants representative of twig-inhabiting forms, such as species of *Pseudomyrmex*, are not found here. One nest, taken from a flower stalk, was between two nodes of the sawgrass stem. Part of the segment was broken through, and this had been replaced with black debris, probably from rotting sawgrass blades.

In hydric hammock its nesting sites were under the mat of a *Sabal palmetto* trunk, in the top of the atrophied root system, and in a stump. In swamp, the ant was found in a fallen log. The nest ramified into many passageways, and occupied three feet of the log which had a diameter of two to two and one-half inches. A dealated queen was taken while it was wandering in one of the buildings of the Reserve.

One colony taken in marsh was found to contain 290 workers, 3 queens, eggs, 218 larvae, and 22 pupae. The arrangement of the castes in this colony, taken in a sawgrass flower stem, is of interest. All of the nest was contained between two nodes of the vertical stem. An estimated one-half of the colony was in the upper half of the segment. Larvae, attached by their

anterior ends, were jutting out into the hollow of the stem. At the top of the section, clinging upside down to the nodal membrane, were many workers and a queen, along with many eggs.

Immature forms have been found in the nests from July through November, but probably occur in all months of the year. Alate and dealated females have been taken in August and September. No information has been obtained for the males.

STRUMIGENYS LOUISIANAE Roger

S. louisianae has been found rarely in turkey oak, bluejack oak, xeric hammock, mesic hammock, and river swamp. It is more common on the Reserve than most species of the closely related *Smithistruma*. As with *Smithistruma*, the most successful means of collecting has proven to be by use of a Berlese funnel. It has, however, been taken from nests in fallen sweetgum (*Liquidambar styraciflua*) logs in which the wood was fairly dry, and in a differential state of decay. It was taken also from the moist wood debris inside a *Magnolia grandiflora* log. Berlese collections were made between temperatures of 24-30° C and relative humidities of 50 and 95%. As in the case of *Smithistruma* on the Reserve, the relative humidity was always above 50% at the time of collection.

In the Gainesville region all of the collections of this species were made in logs of *Magnolia grandiflora* well along in the process of decay. The frequent collections in magnolia may indicate a preference for the moist debris found in these logs.

The ants of this species, like those of the species of *Smithistruma*, are difficult to locate in the field. Their color, which is like that of the wood in which they nest, and their habit of remaining very still in their nest after it is opened greatly enhance the chances of overlooking a nest. Like *Smithistruma* also, they move with a slow, deliberate gait.

SMITHISTRUMA Brown

In 1948, Brown erected the genus *Smithistruma* to receive most of the forms which had previously formed the subgenus *Cephaloxys* of *Strumigenys*. *Cephaloxys*, however, has been shown to be preoccupied, and *Trichoscapa* is the next available name for the group. Brown, however, recognizes that the type species of *Trichoscapa membranifera*, is distinct from the rest of the group. He has therefore raised *Trichoscapa* to the rank of genus, and has introduced *Smithistruma* as a new genus. Creighton (1950), although he was undoubtedly aware of the revisionary measures undertaken for *Strumigenys*, makes no note of them.

Ants of the genus *Smithistruma* build nests only one or two inches in diameter, sometimes deep in the wood. Careful searching is usually necessary in order to find their nests. The color of the ants, which is very much like that of the material in which they live, and their habit of remaining very still when their nests are broken open, make it necessary to look at a nest for several seconds before the ants are seen.

It will be noted that although the temperatures varied widely at the time

of collection the relative humidity was in all cases above 50%. In most cases too few collections were made to draw any conclusions concerning preference of stations.

SMITHISTRUMA BUNKI Brown

The single collection of *bunki* was made from turkey oak. The collection was made by use of a Berlese funnel from litter gathered on an overcast day when the temperature was 37° C and the humidity 66%.

SMITHISTRUMA CLYPEATA (Roger)

S. clypeata was taken occasionally in xeric hammock from Berlese samples. Two dealated females were taken with workers in one sample. It is possible, therefore, that the nest was in the leaf litter, or on the soil under the litter. This collection was made at 18° C and 54% relative humidity.

SMITHISTRUMA CREIGHTONI (M. R. Smith)

S. creightoni has been found occasionally in xeric hammock and rarely in bayhead. All collections were made by means of a Berlese funnel from litter taken at temperatures ranging from 21 to 30° C and relative humidity ranging from 50 to 80%. The litter sample from bayhead yielded the following ants along with the *Smithistruma*: *Solenopsis molesta, Brachymyrmex depilis,* and *Pheidole dentigula.*

SMITHISTRUMA DIETRICHI (M. R. Smith)

S. dietrichi was taken occasionally in turkey oak and rarely in bluejack oak. In turkey oak, one collection was made of several individuals in a log of *Quercus laevis* which was in an advanced stage of wet rot decay. Other collections were made by means of a Berlese funnel at temperatures between 30 and 40° C and relative humidity between 50 and 70%.

SMITHISTRUMA ORNATA (Mayr)

Two collections of this ant were made, one from scrub and one from mesic hammock. The collections were made at temperatures of 28 and 33° C, with humidity of 80 and 98%. Although two collections probably do not indicate the habitat preference of this ant, it can be noted that they were both made under more or less mesic conditions.

SMITHISTRUMA PULCHELLA (Emery)

This species was found rarely in both xeric hammock and river swamp. One collection was made from a Berlese sample with a temperature of 14° C and 75% relative humidity on an overcast day. Specimens were also taken from a mammal trap baited with oatmeal and peanut butter when the temperature was 25° C and the relative humidity was 87%.

SMITHISTRUMA TALPA (Weber)

S. talpa was taken rarely in Pomello scrubby flatwoods, mesic hammock, hydric hammock, and bayhead. In bayhead a nest was found in slash pine

(*Pinus elliotti*) bark at the base of the living tree under litter and just below the soil surface. There was some debris in the nest, and the bark was moist. Other collections were made from Berlese samples between temperatures of 19 and 27° C and between 60 and 65% relative humidity.

TRACHYMYRMEX SEPTENTRIONALIS SEMINOLE (Wheeler)

This fungus-growing ant was found to prefer the higher, drier areas. It was taken commonly in turkey oak and xeric hammock; occasionally to commonly in bluejack oak; occasionally in scrub, Leon scrubby flatwoods, and Pomello scrubby flatwoods; and rarely in mesic hammock.

Areas with little or no litter are preferred by *seminole*, although it has been taken in sand beneath litter, and Cole, in the Great Smoky Mountains, found it beneath stones. Characteristically the colonies build an incomplete crater around the nest openings. Some nests, however, were found with complete craters, and others with no craters. Even in light litter the ants built craters, piling the sand pellets on the surrounding leaves; in heavy litter the craters become obscure.

Incomplete craters faced no common direction. An average crater is 6 to 8 inches in outside diameter, and about 2 inches at the highest point. Nests always have only one opening. No records of the ant were made other than in the subterranean stratum.

A nest of this form, collected in December, 1949, contained 382 workers and 1 queen. All of the workers, except a very few, were clustered about the queen in a deep chamber 4 feet below the surface. The passageways went down to about 6 feet, but no immature forms were seen. The deeper, vertical passageways (3 to 6 feet) were widened at places for several inches so that it would have been possible to place a 2-dram vial within the gallery. Other nests were opened during the same week, and in all of the nests the majority of the individuals remained well below the surface; only a few were seen excavating. The top galleries and chambers of most colonies were empty. In the nests which were active, workers were bringing to the surface organic substances which might have been used fungus substratum. Some nest openings, and other nest passageways were closed, and in three nests small rod-shaped particles were seen clogging the nest openings. These particles were fragments of sedge or grass (probably *Aristida stricta*). Mixed with these were many more unidentified plant fragments. Only very poor evidence of fungus was visible.

Immature forms occur during all except the winter months. Winged forms have been collected in April through July. At 5 P.M. on July 8, 1948, an overcast day, females were seen coming from a nest in turkey oak. Both the attendant workers and the females were very excited. At about 5 minute intervals the females flew off from slightly raised objects near the nest; they showed a special preference for a raised twig near the nest opening. Each female rose almost straight up into the air in a zigzag fashion, until she was out of sight above the treetops.

T. septentrionalis seminole moves only moderately fast while foraging, but it is deliberate in its movements. It usually does not attempt to hide when disturbed, but becomes immobile, and depends on its rough integument

and tubercles to protect it. Foraging is almost completely stopped during late December and January.

The ants characteristically carry leaves slung over their heads. Workers have also been observed taking seeds back to their nests. On several occasions they were observed carrying away seeds which had been discarded from *Pogonomyrmex badius* mounds; this activity always took place at night when the *Pogonomyrmex* nest was closed. Hymenomycetous fungi growing in a lawn also attracted them, and they carried pieces of them back to their nests.

On one occasion this form was found associated with a nest of *Solenopsis geminata* under a log. Species of Corrodentia have also been picked up with collections of *seminole*.

Subfamily DOLICHODERINAE

DOLICHODERUS PUSTULATUS Mayr

D. pustulatus is one of the few ants taken more than three times that occur in only one station. It was found occasionally to commonly in marsh Perhaps more collections around the margins of low, wet places, such as flatwoods ponds, will reveal its existence there also. The species has been recorded northward to New Jersey.

Collections were made most often in various portions of the herbaceous stratum, while others were made from shrubs: a nest between septa of rotting *Sagittaria* stem; sawgrass flower stem; twigs of buttonbush (*Cephalanthus occidentalis*).

Winged forms are present in the nest from September to February. Immature forms were found in the nests in all months.

The speed of movement of the workers is moderate to considerable and their size and behavior is somewhat like that of the subgenus *Colobopsis* of *Camponotus* living in similar nesting sites in marsh.

IRIDOMYRMEX HUMILIS Mayr

This, the Argentine ant, has not been collected from the Reserve but was collected from Palatka, 17 miles to the north of the Reserve. Dr. Smith informs me that the ant was found at Palatka about 1932 when the Bureau of Entomology was scouting for the ant there. It has been reported from there at other times since then, and was taken there by the author in July, 1948, and on February 17, 1950. It appears commonly along the sidewalks of the town, and nests can be taken from under many stones. It probably makes nests also under the sidewalks.

The ease with which the dispersal of *humilis* takes place is indicated by the numerous individuals in the following circumstances. A station wagon with a wooden body had been left in Palatka for several days in the same spot. When the automobile was driven back to the Reserve, it was noticed that many ants had piled sand between the door and the door casing, and had established themselves there, as well as in other places in the station wagon. In all likelihood, the adaptiveness of this ant allows it to move this way into ships, trains, and other means of transportation, and thus extend its distribution.

IRIDOMYRMEX PRUINOSUS (Roger)

Eight stations were occupied by this ant. *I. pruinosus* occurred commonly in turkey oak, Leon scrubby flatwoods, longleaf pine flatwoods, and black pine-fetterbush flatwoods; commonly to occasionally in xeric hammock; and occasionally in bluejack oak, scrub, and Pomello scrubby flatwoods. It seems to prefer areas where its nests are almost never in shadow, whether in the high turkey oak or low black pine-fetterbush flatwoods. The highest numbers of nests occur in stations where there are open areas almost or entirely devoid of litter.

This ant can be found most often in the subterranean stratum, but also in the surface stratum. Most of its nests in sand are either rudimentary or incomplete craters, but there are instances when the nests are found with no crater or with complete craters. Some of these nests occur under litter, while others are built around the bases and root systems of shrubs. It occurs about equally often under the bark of fallen logs and dead stumps, and is also found in litter. The nests under bark are most often built in the debris which occurs between the bark and the rest of the wood. The immature forms, as well as workers, are found in this debris. Several nests were constructed both in logs and in sand.

Immature forms can be found in the nests in all months. Winged forms have been taken in May through July.

When the ants become active in the summer and fall months, or in the other seasons of the year, they form characteristic trails across the sand, extending them sometimes into the vegetation. Each individual is energetically keeping up with the ant ahead, making a more or less straight and lengthy column. Such trails are exemplified by an instance in bluejack oak. Two columns, at an angle of 180° to each other, originated from the same nest. Both columns seemed to have worn a path through the litter. One column was followed for six yards, where it split, sending one branch at least twenty feet up into one bluejack oak, and the other up into another bluejack oak. The other column was followed into litter where it dispersed. When the ants are moving very fast under the influence of the sun, they follow a zigzag pattern, especially on vertical surfaces.

Some of the nests in wood have been associated with termites. The significance of the association is unknown.

DORYMYRMEX PYRAMICUS FLAVOPECTUS M. R. Smith

The confusion which has resulted from recognizing color variants in *Dorymyrmex* has been discussed under the section dealing with the subspecies *pyramicus*. Since two subspecies of the same species have been found in the same area and in identical nesting situations, it is probable that this region is an area of intergradation. In fact, specimens have been found which appear to be intergrades between *pyramicus* and *flavopectus*. More exact identification of intergrades cannot be made until types of both *pyramicus* and *flavopectus* are seen.

Although no specimens of this form have been found on the Reserve, nests have been collected in Salt Springs, Marion County, across the St. Johns River from the Reserve, and in the town of Welaka. A typical nest

was taken in an orange grove from a crater 4 inches in diameter; 1/4 to 1/2 inch in height; and with one opening 1/8 to 1/4 inch in diameter.

DORYMYRMEX PYRAMICUS (Roger)

The material listed under this heading was determined *D. pyramicus* var. *flavus* by Dr. M. R. Smith. Creighton (1950), however, in dealing with the species *pyramicus*, has discarded color as a separatory character and has found certain structural characteristics, such as the shape of the mesonotum, to be clear-cut and constant. Because color was proved to be inconstant, he has synonymized all color varieties.

However, all of the specimens that have the color which is supposedly characteristic of *flavus* cannot be grouped together on morphological grounds. Some of them are the lighter color phase of *pyramicus*, while others are Smith's *flavopectus*. In determinations for the author, Smith, stressing color, evidently recognized a different aggregate of specimens as his subspecies *flavopectus* than Creighton recognizes as *flavopectus* in his 1950 paper. This discussion will follow Creighton by using structural differences as separatory characters.

These ants prefer open sand, and nests have been taken occasionally to commonly in turkey oak and xeric hammock, and rarely in bluejack oak. The great majority of nests were complete craters in open areas. Colonies were also found in a few rudimentary craters, one nest under a log, and another craterless nest with a leaf over the opening. Complete craters of these ants vary from 2 1/2 to 4 inches in diameter; from 1/4 to 3/4 inch in height; and always have one opening to each nest.

Winged forms of this group have been seen May through August. A flight was observed on July 28, 1949.

Ants of this group are very agile and are able to climb vegetation. Their foraging sometimes extends into the night. One colony was found in association with a queen of *Camponotus socius*, taken with the nest only 4 inches below the ground surface.

TAPINOMA SESSILE (Say)

The distribution of *T. sessile* indicates that it is influenced by man. Although in other parts of the country it is widespread, on the Reserve it was taken in only one plant association. This one collection was made in marsh along the St. Johns River, where it is possible that it became established after being transported by man. In this connection, *T. sessile* was recorded from floating islands in the Gainesville region. Several males and females were attracted to light in the buildings on the Reserve. Females were taken in March and July, and males in April.

Cole (1940) gives a good account of the nesting habits of *T. sessile* in the Great Smoky Mountains:

> It was confined for the most part to rather open situations, although nests have been observed in dense moist woods. The ants nest in the soil beneath stones, logs, stumps and strips of bark. The nests are shallow affairs extending no more than an inch or two beneath the soil surface. Most of those in the Park were under rather large flat stones loosely appressed to the soil. Beneath such a cover the orange colored brood was confined to pockets in the soil, or to superficial chambers made by the workers, or very frequently scattered along one inner margin of the stone and mingled with detritus. The colonies were generally populous.

Subfamily FORMICINAE

BRACHYMYRMEX DEPILIS Emery

In its distribution in plant associations, *B. depilis* shows a preference for all types of flatwoods, although its occurrence was high in other associations. It occurs most often in longleaf pine flatwoods, Plummer slash pine flatwoods, and black pine-fetterbush flatwoods, where nests were recorded commonly. *B. depilis* was found occasionally in turkey oak, bluejack oak, scrub, Leon scrubby flatwoods, Pomello scrubby flatwoods, Rutledge slash pine flatwoods, mesic hammock, hydric hammock, and bayhead. There seems to be no reason why it should not also be found in xeric hammock and river swamp.

Most of the nesting sites of *B. depilis* were in the surface stratum. Those nests in sand were associated with wood. Many nests, recorded from logs were taken partly from sand although their major portions were in buried wood. Other nests associated with sand were in the roots of shrubs or other plants. It is probable that these ants were attending aphids.

The most important nesting sites for *B. depilis* on the Reserve are in the bases of living trees and in fallen logs. Other nesting sites in order of preference are: 1) in stumps, 2) in palmetto roots on the surface, 3) in living palmetto roots, 4) under logs, and 5) under litter. They have also been found in sand among the roots of living shrubs, and in sand among fern roots. Nests can be found in wood in a variety of stages of decay, but they occur mostly in or near hard wood. *B. depilis* was taken commonly from burned or charred wood. In most cases the wood was wet or moist.

Many of the nests of *B. depilis,* especially those in the bases of living trees, are in sections as explained under *Crematogaster minutissima missouriensis.* They contain about the same number of individuals as do nests of the latter ant. Immatures of *B. depilis* can be found in all months. Winged forms have been recorded from May to July.

Molasses traps attract this usually slow moving ant. It has been found nesting in close proximity to *Ponera trigona opacior.*

CAMPONOTUS CASTANEUS (Latreille)

This species has been taken in eleven stations, but never with more than occasional relative abundance. It may yet be found in one or two more plant associations, but it is unlikely that it will occur in marsh. *C. castaneus* shows a preference for mesic and hydric conditions. It has been taken occasionally in scrub, Leon scrubby flatwoods, Pomello scrubby flatwoods, Rutledge slash pine flatwoods, xeric hammock, mesic hammock, river swamp, and bayhead; and rarely in longleaf pine and Plummer slash pine flatwoods, and in hydric hammock. In xeric associations, its nests are only in the more moist situations. There is reason to suppose that further collecting will show a higher relative abundance in hydric hammock.

Nests of *C. castaneus* have in all cases been in the surface stratum, in logs or dead stumps. It prefers the last, moist stages of decay, and has been found only in logs of broadleaved trees. Nests will probably also be found partly in the soil, associated with a log or other cover.

The largest colony counted contained only 22 workers and a queen, along

with eggs and larvae. This nest was in all likelihood young; other nests have been seen which were estimated to contain between 100 and 200 individuals. Females have been observed in the nest in February and March, and males in February through May. A mating flight was observed on March 22. Females have been caught on the wing in February also, and males have been caught at light traps in March through May. Immature forms occur in all months.

C. castaneus is an energetic forager. When the temperature drops and the relative humidity rises, it increases its speed of movement, indicating its nocturnal tendencies. It often forages in open areas, such as firelanes, near the mesic or hydric site of its nest. It is one of the ants which temporarily ceases activity during winter months.

Observations on five workers and a number of cocoons of both worker and reproductive castes, brought into the laboratory from a well-decayed log in bayhead, have yielded miscellaneous data concerning the habits of the ants. The ants were kept in a glass and plaster of Paris nest, and for the first month no food was given them. When the cocoons were placed in the nest they were mixed with debris from the original nest in the field. Within a few hours, however, the cocoons had been moved from the debris into the open at one side of the nest, indicating no desire to avoid light. On the second day the cocoons were more disseminated; some were placed by the workers near the sponge; some were under debris; but most were still in the original pile.

On the third day callows began to emerge. In the cases of the several watched, an attendant worker broke open each cocoon, pulling little by little at the cocoon, at the same time dragging the pupa over debris and around the nest. In several cases there was more than one worker attending a cocoon at one time. In the process of removing the insect from the cocoon, the cuticle fitting tightly to the pupa was eaten away by the nurse. The procedure took an hour or more. When the callows first emerged, they were very uncoordinated, and remained bunched together in one portion of the nest.

What were evidently acts of regurgitation were carried on between the newly arrived callows and the workers. In this operation the heads were set at an angle so that one mandible of each ant could be placed on the clypeus of the other, while the other mandible was placed under the head of the other ant. One antenna of each ant intermittently stroked the clypeus of her partner, and the other stroked the under side of the head. Pairs of ants remained in this pose for extended times. Four days after their emergence, the callows assumed the coloration of the other workers.

One week after the ants had been brought into the nest, several callows, partially emerged, had been eaten. All of the discarded cocoons, as well as the partially eaten callows were piled near the sponge.

When food was introduced a month after the workers and immatures were first put into the nest, the workers undertook to feed a winged female callow. This female was much less violent in receiving her food than was a queen of *Camponotus abdominalis floridanus*. The female used her antennae only slowly and inconsistently, and while she did make use of her forelegs, they were more for support on the worker. In distinction, the female of *C. abdominalis floridanus* stroked the worker partner hurriedly, especially

with her forelegs. The heads of the *castaneus* female and worker were in much the same position as that described above for worker and callow. The female would, however, at times invert her head under the head of the worker.

CAMPONOTUS SOCIUS Roger

In 1932 Wheeler described *Camponotus socius* var. *osceola* from Florida. He separated it from *socius* by reason of three yellow stripes on the gaster as compared with two in *socius*. During the present work, it has been found that individuals from the same nest appear with the third yellow band either almost or quite indistinguishable or else strongly evident. Creighton (1950) is therefore followed in synonymizing *C. socius* var. *osceola* with *C. socius*.

This ant prefers the high, dry areas to the exclusion of the wetter environments. It was taken commonly in turkey oak and xeric hammock; and occasionally in Leon scrubby flatwoods and bluejack oak. Like *Aphaenogaster ashmeadi*, *socius* can be found almost always in situations where the litter is relatively light.

All nests of *socius* were taken in the subterranean stratum. A majority of them were in the open where there was no litter. None of the colonies maintained a recognizable crater, although around some nest openings there were rings of sand pellets in what were the beginnings of craters. Nest openings are often found at the bases of turkey oak (*Quercus laevis*); these nests go down into the root systems of the oaks where the rootlets may offer support to the nest chambers and food for the associated aphids.

In turkey oak and xeric hammock *socius* is, on hot summer days, the most conspicuous ant on account of its constant and excited above-ground activity. Its large size and quick movement, along with its habit of moving on top of the litter, make it much more conspicuous than a relatively reclusive ant such as *Odontomachus haematoda insularis*. During the winter months, even though both day and night remained warm, and often became very hot, the above-ground activity of the ant ceased almost entirely.

The feeding activities of the ant are varied. Specimens were taken in November, 1946, by Mr. J. C. Moore from a fox squirrel nest, 26 feet above the ground in a turkey oak tree, where the ants were probably feeding on other arthropods. The species is always attracted to molasses traps in favorable plant associations.

A queen of *C. socius* was taken into the laboratory and placed in a artificial nest on October 19, 1949. She was given nothing but water. During the time she spent in the nest she repeatedly laid eggs, but none of them developed beyond small larvae. On February 2, 1950, two *Camponotus abdominalis floridanus* larvae were placed in the nest, and were accepted by the queen. On the next day, a pupa and larva of *Aphaenogaster macrospina* were put in the nest, and although the queen did not accept these, she did not appear to reject them. However, on the following day, the introduced pupa was destroyed or eaten. The larvae were cared for until March 15, when they also disappeared. On June 30, after 8½ months without food other than the sustenance the larvae and pupa may have provided, the queen died.

Leptothorax texanus davisi was found associated with this species on

October 19, 1949, in turkey oak. A nest of the *Leptothorax*, including a queen, was taken along with a lone queen of *Camponotus*. No crater or nest opening to the sand nest was visible. *C. socius* has also been reported as a casual in the burrows of the Florida pocket gopher (*Geomys floridanus*) (Hubbell and Goff, 1939).

CAMPONOTUS NEARCTICUS Emery

It is not entirely clear from the work of the present study whether or not Wheeler's *C. caryae rasilis pavidus* ought to be synonymized with *nearcticus*. The two variants have been quite distinguishable on the basis of their color, and have occurred in entirely different stations, the black variant nesting in open situations, the lighter variant, *pavidus*, nesting in the shaded mesic or hydric situations.

The problem as to what the relation of the two variants is, would then present itself. It would perhaps be possible for *pavidus* and *nearcticus* to be ecological subspecies, or along the same line, it would be possible for the two variants to have undergone ecological isolation and already be species. However, ecological subspecies and speciation are not well founded in formicid systematics.

In addition Creighton (1950) brings out the point that there exist several named varieties of *caryae* [*fallax*] which are based on slight color differences. "Each is admittedly transitional in this respect. In each the definitive color characteristic was known to vary in the type series." If this be true, there seems little reason for recognizing *pavidus* and *nearcticus* as separate forms on the basis of color distinctions. In this discussion *pavidus* is synonymized with *nearcticus*.

C. nearcticus was taken occasionally in turkey oak, bluejack oak, Pomello scrubby flatwoods, longleaf pine flatwoods, mesic hammock, and river swamp; and rarely in scrub and bayhead. It may also be found in other stations where the trees provide branches as arboreal nesting sites.

Nests in the arboreal stratum are characteristic, but on one occasion a nest was taken in an oak log which had been caught in an oak branch and was supported by the ground at an 80° angle. The black variants of *nearcticus* prefer small branches of pine in open areas, although some were taken in twigs; the wood was usually in the first stages of decay. The lighter variant, on the other hand, was found nesting in small branches of hardwood trees, generally in shaded mesic and hydric areas. It is possible that in the more intense light of open areas the ants take on a darker appearance than in the more shaded hammock areas.

The number of workers in 4 nests of *nearcticus* varied from 28 to 91, averaging about 69 workers per nest. Another, probably incipient nest, contained 12 workers. In only this last was the queen taken. Immature forms have been observed in the nests in both summer and winter. Winged forms have been found in the nests and on the wing from March through July.

C. nearcticus is not a conspicuous forager, but it can at times be seen climbing hurriedly on the trunks of pines or oaks. Workers were discovered by Mr. J. C. Moore in a fox squirrel nest 45 feet above the ground in a turkey oak stand. Mr. Moore states (communication): "Certain beetles, lepidoptera,

and stratiomyid fly larvae were much more abundant than the ants in the wet, rotting interior, 90% of which was Spanish moss." The workers in this case were probably foraging for food in the squirrel nest.

The ant has a tendency to become active on cloudy days. Foraging continues into the night, and workers have been attracted to light traps.

The spider, *Europsis funebris* Hentz (det. W. J. Gertsch), of the family Theridiidae, was taken in a nest of *nearcticus*.

CAMPONOTUS, subgenus COLOBOPSIS Mayr

Most of the *Colobopsis* on the Reserve seem to be more closely allied to either *pylartes* Wheeler or to *impressus* Roger than to any others of the known species from the United States. As Wheeler (1940) admits, *pylartes* is very close morphologically to *impressus* Roger. Wheeler distinguishes the two forms of *Colobopsis* on the basis of the shape of the thorax in the soldier and worker, and in the coloration of the gaster which is banded basally with yellow in *pylartes*. Comparisons of soldiers and workers from the same nest with the descriptions of *impressus* and *pylartes* given by Wheeler show that individuals from the same nest seem to vary between the two species in regard to the conformations of the thorax and the coloration of the gaster. The intra-nest variation is such that the *Colobopsis* found on the Reserve could not be unmistakingly identified; they are treated under one heading.

A third form which shows variation in a different manner was found on the Reserve, but because only a few specimens were taken, it is not included here. Although this third form has a resemblance to the other *Colobopsis*, the major worker or soldier measures only 3.1 mm in total body length, in comparison to 4.3-4.6 mm for *impressus* and 4.5-5.0 mm for *pylartes* (Wheeler, loc. cit.).

Ants of the subgenus *Colobopsis* on the Reserve prefer mesic and hydric situations in which there are vines or other suitable broadleaved twig vegetation. Ants closely resembling *pylartes* occur commonly to abundantly in marsh; occasionally to commonly in mesic hammock; occasionally in scrub, Pomello scrubby flatwoods, xeric hammock, hydric hammock, river swamp, and bayhead; and rarely in Plummer slash pine flatwoods and Rutledge slash pine flatwoods. Nests were arboreal in a great majority of cases, but two nests were found in sawgrass flower stalks, and several were in planted bamboo stalks. Nests were found in greatest abundance in twigs, much less often in galls, and only once in a small branch. Nesting sites of all *Colobopsis* on the Reserve are similar.

These ants, as well as some *Crematogaster* and *Solenopsis*, subgenus *Diplorhoptrum*, nest in "sections" defined under *C. minutissima missouriensis*. A good example of this type of nesting was observed in a planted patch of bamboo. Although the several nodes in the middle of the stalk had been permeated by the ants, many of the other nodes which the nest included were intact, and the nest was thus split into sections.

A count of 10 nests reveals a range in number of workers from 15 to 269; in soldiers from 1 to 72; in totals of workers plus soldiers from 16 to 341. The average of the total numbers of workers and soldiers was about

108. Queens were absent from all but one of the nests counted. Female pupae were observed in the nests in April through June, and adult females were taken over the same period. Males were found in the nests in April and May, and again in November. Immatures occur in all months, except during cold spells. All forms of *Colobopsis* on the Reserve seem to follow this general outline of life history.

When this agile ant makes a nest of a bamboo stalk, as explained above, it cuts a circular nest opening through the internodes of the stalk somewhere near the center. The planted bamboo thickets are a favorite haunt of the downy woodpecker (*Dendrocipus pubescens*). In seeking ants these birds made a characteristic hole in the bamboo stalk. Each hole was about ¼ inch in vertical length and ⅛ inch in width. Most of the woodpecker holes were near the nodes, in contradistinction to the position of the ant-made holes. Two theories for the position of these holes were advanced by Mr. W. M. McLane who observed the actions of a bird eating the ants from a stalk: 1) the bird may find more support in gripping the node; and 2) the stalk nearer the node will be more resistant to bending and will be more easily broken through. If the last is the sole reason for the position of the holes, it would show great keeness on the part of the bird in selecting a spot to peck.

An interesting record was made of an ant which more closely resembled *impressus* than *pylartes*. All pupae observed in *pylartes* nests were naked. But pupae taken from the former nest were in cocoons. One cocoon contained five individuals.

CAMPONOTUS ABDOMINALIS FLORIDANUS (Buckley)

C. abdominalis floridanus prefers the better drained areas of the Reserve, especially turkey oak and xeric hammock, as well as black pine-fetterbush flatwoods, but it is one of the three ants which have been found in all plant associations studied. Nests occur commonly in all stations except Pomello scrubby flatwoods, Rutledge slash pine flatwoods, river swamp, bayhead, and marsh in which they appear occasionally. This even distribution in stations is matched by its occurrence in all strata and in a large number of nesting sites.

Within the strata the ant shows a definite preference for the surface stratum, although it has been found over a third as many times in sand, in a majority of cases under some sort of cover. Relatively few records were made of nests in grass, trees, and shrubs.

The most strongly preferred nesting sites are in logs and stumps. Well preferred also are situations under logs, and under litter. Nests are found often in and under logs, in litter, in palmetto roots on the soil surface, under the mat of palmetto roots and trunks, in the bases of living trees, around roots of grass clumps, in small branches. Other nests have been recorded from open sand with rudimentary or no crater, from between sawgrass blades, from sawgrass flower stalk, in the wall of a building behind cement, under a dead frond resting against a cabbage palm three feet above the ground surface and in the stub of a live oak limb ten feet above the ground.

The types of wood in which *C. abdominalis floridanus* nests vary consider-

ably. Records have been made from logs and stumps of pine and broad-leaved trees, with or without bark, and either charred or unburned. The wood ranges, moreover, from the first stage of decay to the later stages, although the latter seem to be preferred. In many cases the wood is moist, but nests occur in dry as well as wet wood. Most colonies permeate a whole section of log or stump and occupy both the area under the bark as well as most of the wood itself, but nests have been found solely in one position or the other. Records show that the ant is characteristically taken from chambers in the wood, especially in stumps, where a part of the nest will occupy the root system, and another part, chambers in the sand; many colonies extend to higher levels in the wood. Likewise, nests recorded from sand are usually taken from chambers in the sand, a majority of which, however, are associated with roots or wood sunken into the soil, and most do not seem to have been built by the ant.

Mr. J. C. Moore took specimens of this ant on several occasions from fox squirrel (*Sciurus niger niger*) nests in turkey oak. He indicates that in at least one nest, 21 feet high in a turkey oak, the ants were evidently permanently occupying the chamber of a squirrel nest made of twigs and leaves. As he broke open the nest, the ants were seen to pick up their immatures and carry them to safety.

A typical nest of this ant, counted in February, contained 726 workers, as well as immatures. Immatures seem to be present in all months, although in absence of some forms seems to reflect cold weather. Flights of males have been observed in June through August, and in March. Flights of females were recorded for June through August, and in May. Reproductive caste pupae were observed in the nests in October. Nests with a lone queen have been found as early as February.

A group of females were observed in the process of making a flight at 7:40 P.M., during dusk, on July 13, 1948. No males were observed. The sky was overcast, the temperature was 27° C and the relative humidity was 88%. When observed there were perhaps fifty females to be seen, but the flight had probably been going on for some time. They chose the highest possible places to start their independent flights, crawling onto a tin can on the steps of the building in which the nest was located. Each female made a very short preliminary spreading of wings before the flight. A few attempted flight, but fell over backwards, only to make a second successful attempt. Within a space of ten minutes or so, most of the females had left the steps in flight. They took to the air at a rate of from three a minute to ten or twelve a minute. Each ant ascended at approximately a forty-five degree angle to the ground. Most flights proceeded in the direction in which the ant was headed at the taking-off point, but some swerved in one direction or another, perhaps being caught in a wind current; they always, however, maintained somewhat the same angle to the ground. When the last of the queens had left it was dark. During the whole ceremony many excited workers were in attendance.

On June 29, 1948, an aggregation of males above ground was first noticed because of the excitement of workers traveling in file some distance from the nest. These workers were followed to the nest in a stump in turkey oak

where the males were wandering about the nest site with workers in constant, excited attendance. The males seemed to wander farther from the nest than the workers would permit, for the latter were constantly carrying winged forms back toward the nest opening. Most workers carried the males by grasping them by the head, with their body straight out in front of the worker. Although the nest was watched until it became impossible to see the ants, no flight was observed. The temperature at the time of observation was 25° C, and the relative humidity was 40%.

A dealated female of *C. abdominalis floridanus* was taken nesting alone in a twig, and was brought into the laboratory. Within ten days she had produced ten or twelve eggs and small larvae which appeared in an unsymmetrical sphere. The queen characteristically stood with her head slightly in front of the clutch, seemingly with her palpi on them. From time to time she would rub her antennae over the eggs and then along her forelegs.

When disturbed, the queen would pick up the clutch in her mandibles and pose with it or carry it to some other portion of the nest; the eggs and larvae were always kept in a cleared area. After placing the eggs down, the queen would repeat the actions of moving her antennae over the eggs and then under her forelegs. She consistently avoided the sponge.

It was difficult to tell exactly the length of time immatures required to develop from one stage to the next. There was evidence that at least some larvae and pupae had died or been killed, and new eggs were being laid constantly. Approximate times, under the conditions imposed for the development, were as follows: egg to larva, 21 days; larva to pupa, 20 days; and pupa to worker adult, 8 days. It became apparent after observing another ant queen under conditions of low temperature that the length of the developmental period for any of the immature forms is lengthened by adverse conditions. It can be noted here that pupae of another queen, placed under identical environmental circumstances except for the absence of adult forms, did not hatch.

The first offspring of the former queen were all very small workers. These measured only 5.5 mm. in total body length. No insects this small were observed in large, thriving colonies in the field.

The feeding habits of the queen of *C. abdominalis floridanus* are compared with those of a *C. castaneus* winged female under the latter ant. The small workers mentioned above took water from the sponge and went to the queen. When she encouraged a worker with her antennae, the two ants would assume positions in which the axes of their heads were at right angles, one mandible of each above, and one below the partner's head. The queen stroked violently with her antennae during the regurgitation, and made frequent use of her forelegs. The worker returned the antennal strokes much more slowly, and made no use of the forelegs.

On several occasions, best exemplified in roots of saw palmetto, the immature forms of *C. abdominalis floridanus* have been found at different levels in the nests. In all cases the pupae were at the top, with the eggs and larvae together below, or the larvae placed between the pupae and the eggs.

Most of the year this is a fast moving, excitable ant which finds no difficulty in negotiating the trunks of trees and the stems of herbs. However,

in November, especially in 1948, there was a noticeable cessation in its above-ground activity. During most of the year it is active both in the day and at night, except during rain, when it and most of the other ants seek cover.

The feeding habits of *C. abdominalis floridanus* are rather diversified. It is attracted to liver as well as molasses. On several occasions it has been recorded taking insects to its nest. Workers have been observed actively dissecting insects before carrying them to their nest. Termites, colonizing in many instances the same type of wood as *C. abdominalis floridanus*, perhaps supply food for the ant. When a log which contains both termites and this carpenter ant is broken open, the excited worker ants pick up termites between their mandibles and carry them as if they were their own immatures. This habit has been noted in other ant forms.

C. abdominalis floridanus has been found associated with the following animals: *Odontomachus haematoda insularis; Paratrechina parvula; Myrmecophila?* (Orthoptera); termites (Isoptera); several beetles and beetle larvae (Coleoptera); chilopods; *Hypoaspis?* (Acarina). In this connection it might also be mentioned that on several occasions, dead workers of this ant were found tightly clinging to vertical grass stems, or to strands of hanging Spanish moss. The head of each worker was upward, and from the head or the anterior portion of the thorax a fungus, tentatively determined as *Cordyceps* sp., was protruding. The worker, being attacked by the fungus, and climbing to die above the ground suggests an excellent medium for the dispersal of the spores of the fungus.

When logs which contained this pugnacious *Camponotus* and *Odontomachus haematoda insularis* were broken open, the workers of both species usually became excited and attacked each other. In the field, the *Camponotus* were much superior in battle, killing the *Odontomachus* each time an observed combat took place. In the laboratory, ants of this *Camponotus* introduced into a common container with *Odontomachus* lost as many battles as they won. The sting of the *Odontomachus* seemed to be fatal, but they were less pugnacious than the carpenter ant, using their mandibles to spring away from their adversaries. The *Camponotus*, quicker in the attack, were adept at severing legs and gasters from the bodies of their opponents.

PARATRECHINA LONGICORNIS (Latr.)

The nesting places of *P. longicornis* are very closely associated with the structures made by man, especially in places where trade through seaports is conducted. Its distribution shows that it is a cosmopolitan species.

It was taken in Gainesville, and in Crescent City, 11 miles to the southeast of the Welaka Reserve. In both of these places nests were found in crevices in the cement of walls of buildings, or beneath the cement in the soil at the base of the buildings. Unlike the imported *Iridomyrmex humilis*, nests were always found in buildings, rather than, as in the case of *I. humilis*, outside the buildings in the ruderal sections. Although it was not found in Welaka, it probably occurs there in some sections.

The long, spidery legs of this ant, and the fast, seemingly aimless movements, are the basis for its being termed the "crazy ant" in some regions. It

has been observed to carry spiders to its nest, and to be attracted to candy, and sweets of other kinds.

PARATRECHINA ARENIVAGA (Wheeler)

Creighton (1950) lists *arenivaga* as a subspecies of *melanderi*. All the male specimens in his collection taken in the type locality of *arenivaga* have genitalia more like Wheeler's figure of *melanderi* than like his figure of *arenivaga* (1905). Moreover, he states that "I believe that I have fairly conclusive evidence, from specimens taken in southern Alabama, to show that *melanderi* and *arenivaga* intergrade in that area." On this basis he has made *arenivaga* a subspecies of *melanderi*.

Specimens collected during the present study, however, have genitalia which agree with cotype material of *arenivaga* from the Museum of Comparative Zoology. The genitalia of these males are very similar to the genitalia of *arenivaga* as pictured by Wheeler. Therefore, until it can be certain that Creighton collected *arenivaga*, and not another form in the type locality of *arenivaga*, and until the intergradation between *melanderi* and *arenivaga* can be established without doubt, it seems best to use *arenivaga* as a distinct species.

Although *Paratrechina parvula* becomes very light in color in the higher and more open areas of the Reserve, it can almost always be distinguished from the deep yellow *P. arenivaga*. *P. arenivaga* is slightly larger than *parvula* in most measurements of the workers, and is definitely larger in the winged forms. Two of the best characters for the separation of these two species are the venation of the wings in both the male and female, and the shape of the male genitalia.

Even though *arenivaga* is abundant here, it was not listed by those who have made state lists. Wheeler (1905) remarks that it occurs in New Jersey and near Austin, Texas. Buren (1944) notes that the ant has been taken from the Missouri River bluff, but from no other part of Iowa. This spotty distribution and its occurrence near ports and rivers may indicate that the distribution of the species is affected by commerce. In all instances it builds craters similar to those on the Reserve.

On the Reserve *P. arenivaga* was found in 7 plant associations. It nested abundantly in the high and open areas of turkey oak and xeric hammock, where it was able to find suitable areas for its crater nests. Nests were found occasionally in Leon scrubby flatwoods, and rarely in bluejack oak, Pomello scrubby flatwoods, longleaf pine flatwoods, and Plummer slash pine flatwoods. Colonies were also found often in firelanes and on lawns.

Without exception it was found in the subterranean stratum where it built complete craters. These craters ranged from 1 to 3 inches in diameter and from 1/8 to 1/2 inch in height of the crater. All nests had one central opening. Most of the nests were built in light colored sand which matched the light color of the ant.

The immature forms probably occur in the nests all year. Winged forms appear in January and remain until February or March when the mating flights take place. Activity that seemed to be preparatory to one such flight was observed on February 12, 1950, at 4 P.M., just after a rain when the

temperature was 21° C and the relative humidity was 100%. Although there were many males in the upper chambers of the nests, none was noted taking off from eight nests observed. There was an indication that the nests are sex specific, or nearly so. Many of the workers were in a replete state.

This is a moderately fast moving ant, but on warm, overcast days it tends to increase its speed of movement. It is active during both the day and the night. During the winter months its above-ground activity becomes limited.

Many animals have been found in association with this ant. In the nests mentioned above from which the winged forms were emerging, a black cricket with red markings on its head was observed, but not taken. *P. arenivaga* has been found on quite a few occasions with the following: *Solenopsis molesta; Solenopsis pergandei; Reticulitermes* spp. (Isoptera). The termites were always in small pieces of wood buried in the sand, and the *arenivaga* nests passed through or close by the wood. The *Solenopsis* occupied chambers of the *Paratrechina* nest about one-half to one foot below the surface. On occasion both *Solenopsis* were found in the same nest. One worker of *Pheidole morrisi* was found in a nest of this *Paratrechina,* and several workers of *arenivaga* were found in a nest of *Pheidole morrisi.* Since these ants usually live independently, it is likely that the workers had merely wandered into the foreign nests.

PARATRECHINA PARVULA (Mayr)

P. parvula and *Pheidole dentata* are perhaps the most common ants on the Reserve. However, the ants listed under *P. parvula* in this paper show variation in the worker caste. Some are of very pale or light coloration and small size, while others are darker and of larger size. But some small, dark workers, and large, light workers were found. Moreover, the color of workers within the same colony may be either pale straw with light brown bands on each segment of the gaster and with a dark head, or the gaster and head may be dark brown with the thorax and legs only slightly lighter.

Some of the variation in color is due to the change from the callow condition to the full color condition. Some of the dark workers, as well as some callows, have a distended gaster. Under both of these circumstances the workers have a lighter appearance than they would in their mature, undistended condition.

The male genitalia of the lighter colored form are insignificantly different from the darker form (the former are slightly smaller, but have the same configuration). Wesson and Wesson (1940) have found similar variation in *parvula* in southcentral Ohio:

> Our material shows considerable variation which we have been unable to refer to any but this species on comparison with material in the Wheeler collection at the Museum of Comparative Zoology, Harvard University. Specimens from wooded places are usually dark brown or black and have few or no hairs on the antennal scapes. They agree with the typical *parvula*. Specimens from dry or exposed situations, on the other hand, are usually paler and have a variable number of hairs on the antennal scapes . . . . we have occasionally found colonies in which some of the workers bore a variable number of hairs on the antennal scapes while others bore none, suggesting that this character may not be entirely reliable.

Specimens from the Reserve agree with those from Ohio in that the number

of hairs on the antennal scape is variable. If all of the forms represent one species, it is possible, as the above quotation suggests, that the drier nesting sites will contain lighter forms. But both light and dark forms have been taken from almost every station on the Reserve, although the lighter forms are more prevalent in the higher, drier areas. Conversely, the larger sized workers are found in the wet areas.

In general *P. parvula* seems to prefer the wetter areas, although nests have been found in all of the stations. It was taken abundantly in black pine-fetterbush flatwoods, mesic hammock, and marsh; commonly to abundantly in Plummer slash pine flatwoods; commonly in turkey oak, Leon scrubby flatwoods, longleaf pine flatwoods, Rutledge slash pine flatwoods, xeric hammock, hydric hammock, and bayhead; occasionally to commonly in scrub, Pomello scrubby flatwoods, and river swamp; and occasionally in bluejack oak.

Three-fourths of the records of *parvula* were made from the surface stratum. Approximately equal numbers of collections were made from under cover in sand and from nests in the grass stratum. A few nests were taken arboreally.

Nesting sites of *parvula,* in order of preference, are: 1) in litter, 2) in fallen log, 3) in grass clump, 4) under litter, 5) in bases of living trees, 6) between sawgrass blades; 7) in dead stumps, 8) in palmetto roots, 9) in small branches, 10) in twigs, 11) in and under logs, and 12) under logs.

Nests occur in wood varying from wet to dry, and from the first stages to the last stages of decay. They have been found under bark, in both broadleaved and pine wood.

Most of the nests in sawgrass are between the growing, appressed blades, although some are in the dark stumps of sawgrass which are wet or saturated. In the living sawgrass, the ants are able to live at or near the water surface. Several nests were found slightly below the water surface, within the plant parts which excluded the water. No nests were found very far from the water level, since the blades diverge leaving no place to nest at a height of a few inches; these higher portions of the plants are also exposed to much greater evaporation then the partially shaded areas near the water. In January, the sawgrass is for the most part dead, except for the inside blades and the outer blades fall slightly apart. During this period, even though the temperature is clement, the ants are relatively scarce in marsh.

A similar phenomenon is noted for nests in grass clumps. Beginning in October the grass clumps in which the ants have lived during the summer become dry and completely dead above the soil surface. With the drying out of the grass above the surface, the density of the population in this nesting site decreases. Those ants that remain inhabit the root systems of the grass; the others find litter or logs with suitable moisture. It is possible that during the rainy summer the ants move their nests into the above-ground, higher portions of the grass to avoid supersaturation, and that with the onset of winter and dry weather, with the consequent drying of the grass, the ants move down into the moist lower stems and roots.

The number of individuals in the nests of *parvula* ranged, in the 4 nests counted, from 25 to 72, averaging 45. Females have been taken in nests as early as late July, and as late as the latter part of January. Males were found

in September through the last part of February. Winged forms are most abundant in the nests in October, November, and December. The presence of winged forms during most months is noteworthy.

This moderately fast moving ant is attracted to liver and molasses. Workers of *parvula* forage actively at night. It has been found associated with the following insects: Atelura (?) (Coleoptera); Corrodentia: Psocidae; Diptera: fam.?; *Pheidole dentigula; Solenopsis picta; Crematogaster minutissima missouriensis; Camponotus abdominalis floridanus; Odontomachus haematoda insularis.*

PRENOLEPIS IMPARIS (Say)

P. imparis has been taken in only two plant associations. These are turkey oak, in which it was found rarely, and scrub, in which it was found occasionally. Occasional nests can be found on lawns in ruderal areas; this may be an important nesting situation for the ant. In the Gainesville region *P. imparis* was found occasionally in mesic hammock and ruderal areas, and was also taken in turkey oak and flatwoods.

All of the nests on the Reserve were under litter, even those in the ruderal areas. Those in Gainesville, however, nearly all formed complete craters in open areas. Both Gregg (1944) and Cole (1940) note that the ant builds craters and that it lives in clay. Cole states that "The ants nest is shaded, moist, compact soil, particularly clay, occasionally beneath wood or stones; but more often construct obscure crater mounds consisting of pellets of soil scattered around the single nest entrance." This last type of nest is found under light litter on the Reserve. A nest was observed in which all of the ants were dumping sand pellets at least a foot from the nest opening, in the process of excavation.

P. imparis moves with only a moderate degree of speed. It becomes most active during cloudy or overcast days. Molasses and corn bait for mammal traps will attract it. Talbot (1943a and b) and Wheeler (1930) have made extensive studies on *P. imparis*, in regard to population and response to environment.

FORMICA ARCHBOLDI M. R. Smith

F. archboldi was found in six plant associations. It was taken occasionally to commonly in turkey oak and black pine-fetterbush flatwoods; occasionally in longleaf and Plummer slash pine flatwoods, and rarely in Rutledge slash pine flatwoods and xeric hammock. This distribution indicates that *F. archboldi* is attracted to areas of pine growth, more, it would seem, because of the lack of heavy leaf litter than because of the pines. It has been found to be the most common *Formica* on the Reserve.

It has always been found in the subterranean stratum, and either under a log in the sand or under litter. Of the 2 nests counted, one under a log in black pine-fetterbush flatwoods contained 63 workers, and 4 callows, in addition to eggs, 21 larvae, 18 pupae, and 20 pupal cocoons. The other nest in turkey oak, taken under litter, contained 222 workers, with eggs, 25 larvae, 6 worker pupae, and 21 pupal cocoons. This last nest also had 7 female pupae, 3 female callows, and 20 females. Each nest had a queen.

The first nest was within one foot of the surface, just above the water table. It contained many heads of *Odontomachus haematoda insularis*, indi-

cating that the *Formica* may take over *Odontomachus* nests, or that the *Odontomachus* is used as food. The second nest was 8 to 12 inches below the surface of the soil with a 1/4 inch passageway leading to the chambers. The castes and immature forms seemed to be arranged in order from top to bottom of the nest in the following order: winged females; larvae and eggs; pupae; cocoons of workers; and cocoons of winged forms. It should be noted that pupae are both nude and covered with cocoons.

F. archboldi usually moves with considerable speed in most of the months of the year, but collections indicate that there is a period of inactivity in the winter months. Specimens have been taken with a species of small mite (*Hypoaspis* ?) on the gaster directly behind the petiole. In one nest the cricket *Myrmecophila pergandei* Bruner (det. Cantrall) was found.

FORMICA PALLIDEFULVA Latreille

F. pallidefulva was found on the Reserve in only three plant associations. It was taken occasionally in turkey oak and xeric hammock, and rarely in Pomello scrubby flatwoods. These situations have in common their openness, and absence of thick litter.

All nests of this species were found in the subterranean stratum, all under cover of litter. It has also been collected in Gainesville in this same sort of nesting site.

One nest of *F. pallidefulva* in turkey oak had two openings, one of which led for only a short distance. The main opening led laterally, at a depth of about 1/2 inch, for about 3 inches where there was a chamber, then straight down to where the passageway stopped at 3 feet. Blind passageways, and chambers were spaced along the downward passage. At 3 feet workers of *Camponotus socius* were encountered, and were seen carrying cocoons. No eggs, larvae, or pupae, other than those carried by the *Camponotus* were observed.

Like the other *Formica* of the Reserve, this ant could usually be seen moving with considerable speed in its foraging activities.

FORMICA SCHAUFUSSI Mayr

On the Reserve *F. schaufussi* was found rarely in turkey oak and longleaf pine flatwoods. In Gainesville it was found in xeric hammock and an open ruderal area.

Nests on the Reserve were all in the subterranean stratum and under litter. About this ant, Cole (1940) writes:

> The ants live in the ground, as a rule beneath stones in open, warm, rather dry grassy areas. A few obscure crater mounds were found, and a number of colonies which nested beneath stones had adjoining earthern craters. The stones were loosely banked along their margins with soil particles. Underneath was a number of large, irregular superficial chambers, but the main part of the nest was at a depth of 1 1/2 to 2 feet underground. The colonies are as a rule, populous, and the workers are agile and timid when disturbed.

These remarks agree with, and add to, the observations made on the Welaka Reserve.

SUMMARY

The present study deals with ecological relationships of the ants of the University of Florida Conservation Reserve, a 2,180 acre tract in northeastern peninsular Florida. Field work was carried on from October, 1947, until June, 1950. Seventeen collecting trips were made to each of fifteen areas or stations (plant association-soil type combinations) chosen to represent the major vegetational and soil variations of the Reserve.

Seventy-two species and subspecies of ants were taken on the Reserve, and four others were collected in nearby towns. Fourteen ant forms were recorded for the first time from the state.

Quantitative relationships were determined for the ant forms within the stations, by using the colony, and not the individual ant, as the biological unit. Assemblages of ants which were characteristic and distinctive qualitatively and/or quantitatively were found to exist in the stations, and in four strata and sixteen nesting sites within the stations. The environments of each of these assemblages were therefore designated ant habitats.

For the Reserve, *Pheidole dentata* showed the greatest abundance; the next four forms in order are: *Paratrechina parvula; Camponotus abdominalis floridanus; Odontomachus haematoda insularis; Solenopsis molesta.*

In both variety of ant forms and number of nests, the turkey oak and xeric hammock stations rank well above all others, whereas the slash pine flatwoods, river swamp, and marsh stations rank at the bottom. This indicates that the higher, drier stations are more suitable for ants than the lower, wetter areas.

There were 14 forms collected at only one station, while each of 3 forms was found in all 15 stations. When the ants which were collected only once are omitted, then there were only 5 forms collected at only one station. From this and other evidence it seems probable that ants do not show as much dependence on plant association-soil type combinations as do other animals.

Distribution in strata and nesting sites showed that ants preferred the subterranean and surface strata, and within these strata, nests in sand, fallen logs, or stumps. Only nineteen forms nested in the herbaceous and arboreal strata.

A correlation is shown between the number of nesting sites a form occupies and the number of stations it occupies. In general, however, the number of stations occupied increases faster than the number of nesting sites occupied. From this it would seem that many ants are more restricted by nesting sites than by plant association-soil type combinations.

Data concerning the life histories, activity, food, and habits in general have been brought together under the appropriate ant form in the ANNOTATED LIST. Indications of variations in seasonal occurrence have been apparent for only a few forms, and in all cases have been due to the seasonal variability in abundance of the suitable nesting sites. The ant forms on the Reserve vary greatly in the time and physical conditions under which they forage. Several forms have a wide range in this respect.

It was also observed that the individuals of certain ant forms appear darker in color when they nest in the open areas of the Reserve, whereas other ants

are darker in the shaded areas; and that the individuals of certain forms are larger in the wetter areas than in the higher, drier areas.

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Rhythms of Locomotor Activity and O_2-Consumption of the Grasshopper Romalea microptera[1]

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Rhythmical behavior with a 24.0 hour frequency has been observed in many organisms. In several instances the rhythms depended directly upon illumination changes and were not evident in the absence of normal day-night conditions. However, the rhythmical activity of numerous organisms persisted under conditions constant with respect to light and temperature. Reviews of the extensive literature on 24-hour rhythmicity have been published by Welsh (1938), Park (1940), Kleitman (1949), and Webb (1950).

Past research on rhythms of insects was primarily descriptive. Correlations were drawn between the time of maximum activity in the laboratory, the behavior of the organism in its environment, and naturally occurring environmental rhythms. Lutz (1932) found spontaneous locomotor activity rhythms that persisted in constant darkness in three species of saltatorial orthopterans, *Gryllus domesticus, G. assimilis,* and *Stenopelmatus* sp. The latter was more active about midnight than at other times of day or night. Both species of *Gryllus* were most active near 9 P.M.

The current trend is to elucidate the mechanism of rhythmical behavior. Recently, Harker (1956) has been investigating the locomotor activity rhythm of the cockroach *Periplaneta americana* with considerable success. This investigator showed that the activity rhythm of *Periplaneta* depended upon the rhythmical release of a blood-borne factor from the subesophageal ganglion.

The lubber grasshopper, *Romalea microptera,* readily available in the New Orleans area, is an ideal organism for investigations of insect physiology because of its hardiness and large size. Practically no information concerning the biology of *Romalea* has been published.

Preliminary investigation revealed that *Romalea* exhibited a 24-hour rhythm of spontaneous locomotor activity. Experiments were, therefore, designed to analyze this rhythm and to determine if *Romalea* also has a 24-hour rhythm of oxygen consumption.

Materials and Methods

Nymphs and imagoes of the lubber grasshopper, *Romalea microptera,* were used in the experiments described below. The stock supply of specimens, obtained from the area south of New Orleans, Louisiana, was maintained in laboratory cages exposed to normal day-night conditions. The stock grasshoppers were fed water and lettuce in the cages but were not fed when in activity recorders and respirometers. The sex of the adults was determined when they were used in an experiment but no difference due to the sex of the individuals was apparent from the results. Likewise, the differences in

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the rhythms described below were not due to use of specimens from different stages of the life cycle.

The methods of measuring spontaneous locomotor activity and oxygen consumption were essentially the same as those employed by Fingerman and Lago (1957) in an investigation of the rhythms of locomotor activity and metabolic rate of the crawfish *Orconectes clypeatus*. Locomotor activity of *Romalea* was recorded under an illumination of less than one ft. c. light intensity. The method was a modification of the technique described by Kalmus (1938). A thread was tied about the thorax of a *Romalea* which was then placed in a dish with a wire-mesh top that prevented escape. The string was then tied to a light aluminum lever which recorded movements of the grasshopper on carbonized paper fastened to the drum of a 24-hour kymograph. The drum rotated at the rate of 2.00 cm per hour.

Recording of locomotor activity began between 9 A.M. and 4 P.M. Twenty-four hours later the records were removed from the kymograph and sprayed with "Krylon fixative." Hour intervals were then marked on the records and the movements per hour counted. Because the 24-hour kymograph records started at different hours of the day and graphs based on 11 P.M. to 11 P.M. recordings were desired, the data were rearranged for presentation in figs. 1, 2, and 5-9 as follows. No matter what time of day the recording began the number of movements from 11 P.M. to midnight was counted first and the movements for the remaining 23 hours were recorded in sequence. This method of recording data 1) facilitated comparison of the locomotor activity of individual grasshoppers whose records were started at different times of day and 2) allowed averaging of data obtained with several individuals. The data for each two hour interval beginning at 11 P.M. were averaged. Further support for this method of analysis of the kymograph records was gained from comparison with the oxygen consumption curves. A striking similarity between the activity and oxygen consumption records of normal *Romalea* was evident and the latter were obtained for 24-hour periods beginning at 11 P.M. The similarity of the records obtained for activity and oxygen consumption of *Orconectes* by Fingerman and Lago (1957) lends additional support to this method of analysis.

Oxygen consumption was recorded for 24-hour periods and longer by means of a continuous-recording respirometer designed by Brown (1954). Each respirometer consisted of a collapsible plastic bag attached to a 100 ml Soxhlet flask via a capillary connection. The plastic bag contained sufficient oxygen for one grasshopper for at least three days. Weights were affixed to the flask so that the respirometer would sink just below the surface of the water in a constant-temperature bath maintained at 29° C. As the grasshopper consumed oxygen, the volume of the plastic bag decreased, the specific gravity of the respirometer increased, and the buoyancy decreased. The respirometer, therefore, sank deeper. Increase in specific gravity was recorded by means of a lever system attached to pens recording on a drum that turned at the rate of 2.05 cm per hour. Decrease of the volume of oxygen in the respirometer caused the pen to trace a line continually moving closer to a baseline. The respirometer increased one gram in weight for each milliliter of oxygen consumed. Therefore, the lever system could be calibrated and the volume of oxygen consumed per hour calculated. The method of

analysis and presentation of the data were the same as described in detail by Brown, Bennett, and Webb (1954), Sandeen, Stephens, and Brown (1954), Fingerman (1955), and Fingerman and Lago (1957).

For determinations of metabolic rate vials of 20 per cent potassium hydroxide (carbon dioxide absorbent) and saturated cupric chloride (ammonia absorbent) were placed into each of 10 respirometer flasks. Nine of the respirometers had one grasshopper in each of them, the tenth served as a control. Approximately 50 per cent of the records proved to be usable because an occasional grasshopper would die in the respirometer and because of mechanical failure of the pens or plastic bags. The respirometers were maintained under constant illumination in a windowless room where the light intensity at the surface of the water in the constant temperature bath was .25 ft. c.

Grasshoppers were weighed after removal from the respirometers. The sex of adults and the nymphal stage of immature specimens was recorded. Rates of oxygen consumption were expressed as milliliters of oxygen consumed per gram of grasshopper per hour (ml/g/hr). Data for each two hour interval of a 24-hour period beginning at 11 P.M. were averaged.

EXPERIMENTS AND RESULTS

TWENTY-FOUR HOUR RHYTHMS OF LOCOMOTOR ACTIVITY OF INTACT ROMALEA MICROPTERA

The spontaneous locomotor activity of intact specimens of *Romalea microptera* was determined for 24-hour periods. Twenty-four hour activity rhythms were evident from inspection of the kymograph records. Analysis of the records revealed two types of rhythms. One group of grasshoppers displayed maximum spontaneous locomotor activity in the forenoon and the second group was maximally active in the afternoon. For convenience in discussing the results the rhythm of the group maximally active in the forenoon will be referred to as type A and the rhythm of the latter group as type B.

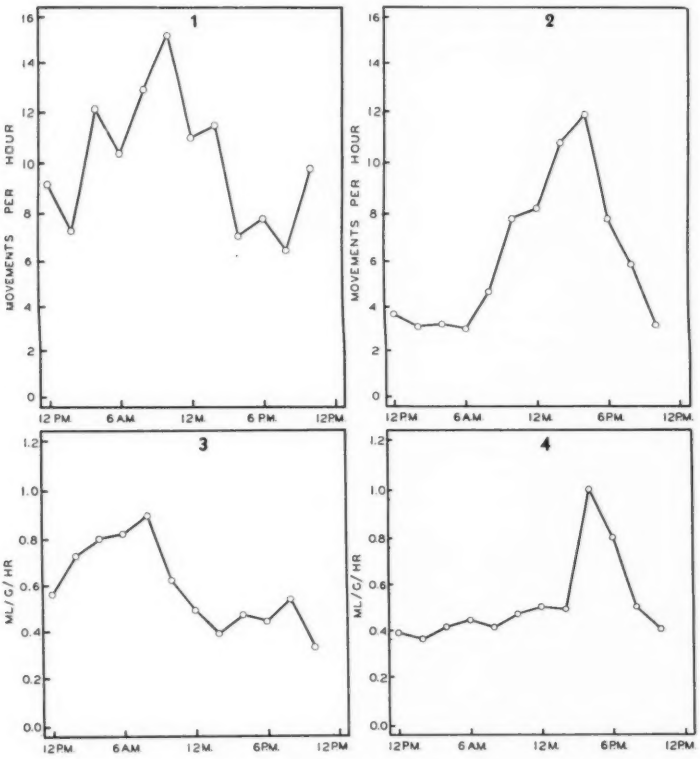
The averaged results obtained with 17 type A and 20 type B individuals are presented in figs. 1 and 2 respectively. The maximum activity of type A individuals occurred about 10 A.M., of type B about 4 P.M., a six hour difference. Minimum activity appeared to occur about 10 hours after the maximum although the precise relationship between the times of maximum and minimum activity could not be determined.

TWENTY-FOUR HOUR RHYTHMS OF OXYGEN CONSUMPTION OF INTACT ROMALEA MICROPTERA

The metabolic rates of 39 normal *Romalea microptera* were determined. Analysis of the data revealed the two types of rhythm observed from the activity records. Twenty-six type A individuals (fig. 3) and 13 type B (fig. 4) were recorded. The maximum of oxygen consumption of type A specimens (fig. 3) occurred two hours earlier than the maximum in the type A pattern of locomotor activity (fig. 1). However, the maximum of the type B oxygen consumption curve (Fig. 4) occurred at the same time

as the maximum activity of type B individuals (fig. 2). The average interval between the maxima of the rhythms of type A and B intact individuals was, therefore, seven hours.

In 12 cases the same specimen was run through both the respirometer and activity recorder. In 11 cases the type of the rhythm, A or B, was the same whether the activity pattern was determined prior to the respiration pattern or vice versa. In the twelfth instance the activity pattern was determined,



Figs. 1-4—1. Twenty-four hour locomotor activity rhythm of intact *Romalea microptera* more active in the forenoon than at other times of day (type A). 2. Twenty-four hour locomotor activity rhythm of intact *Romalea microptera* more active in the afternoon than at other times of day (type B). 3. Twenty-four hour rhythm of oxygen consumption of intact *Romalea microptera* that had a higher metabolic rate in the forenoon than at other times of day (type A). 4. Twenty-four hour rhythm of oxygen consumption of intact *Romalea microptera* that had a higher metabolic rate in the afternoon than at other times of day (type B).

then the metabolic pattern. The latter differed from the former. The activity pattern was then redetermined and this time the pattern was the same as the metabolic pattern. The probable explanation of the original discrepancy was that the grasshopper to be put in the respirometer was accidentally exchanged with another specimen when originally removed from the activity recorder.

TWENTY-FOUR HOUR ACTIVITY RHYTHMS OF ALLATECTOMIZED ROMALEA

Both corpora allata were removed through a triangular opening on top of the head according to the method described by Pfeiffer (1939) for allatectomy of the grasshopper *Melanoplus differentialis*. One day was allowed for the grasshoppers to recover from the anesthesia before they were placed in the activity recorders. The data obtained with allatectomized *Romalea* are shown in figs. 5 (type A) and 6 (type B). Fig. 5 represents the average of seven specimens and fig. 6 the average of 19. Allatectomized individuals showed no impairment of the 24-hour rhythm. Type A and B individuals were found just as with intact specimens. Furthermore, the maxima of activity of type A and B allatectomized grasshoppers occurred at the same times as the maxima of the corresponding types of intact *Romalea*. The total activity throughout the day was practically unchanged in allatectomized specimens. The average of the 24 values shown in figs. 1 and 2 (intact specimens) was 8.1 movements per hour. The corresponding value for the allatectomized specimens (figs. 5 and 6) was 8.9 movements per hour. The corpora allata were evidently not necessary for expression of the activity rhythm.

TWENTY-FOUR HOUR ACTIVITY RHYTHMS OF BRAINLESS ROMALEA MICROPTERA

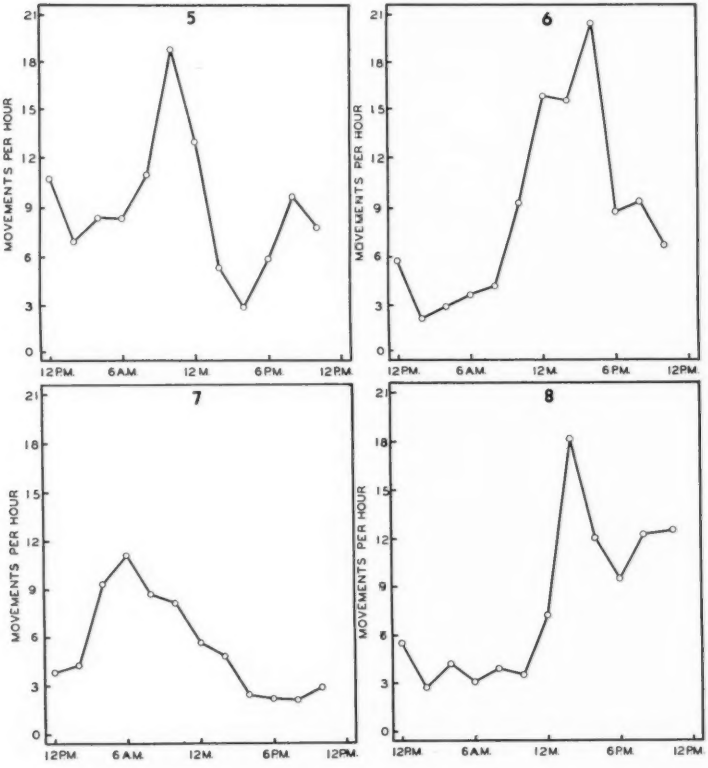
Grasshoppers were anesthetized and opened in the same fashion as those that were allatectomized. The optic tracts and circumesophageal connectives were transected. The brain could then be removed. One day was allowed for the brainless *Romalea* to recover from the anesthesia before they were placed in the activity recorders.

The results obtained with brainless grasshoppers were shown in figs. 7 and 8. Figs. 7 and 8 represent the averages of 14 and 11 individuals respectively. As evident from inspection of these figures brainless *Romalea* also exhibited type A and B rhythms. The brain was evidently not essential for expression of the locomotor activity rhythm. However, the activity of the *Romalea* was slightly less than that of intact and allatectomized specimens. The average of the 24 values shown in figs. 7 and 8 was 6.7 movements per hour as compared with 8.1 movements per hour for intact and 8.9 for allatectomized specimens.

The corresponding times of maxima activity of type A and B individuals were earlier in the day than the maxima of intact and allatectomized specimens (figs. 1, 2, 5, and 6). The maxima for brainless type A and B *Romalea* occurred at 6 A.M. and 2 P.M. respectively.

ACTIVITY OF ROMALEA WHOSE SUBESOPHAGEAL GANGLION WAS REMOVED

The subesophageal ganglion was removed through an opening made in the ventral portion of the cervix of an anesthetized grasshopper after the nerves leading to and from the ganglion were cut. The opening was sealed with paraffin. One day was allowed for recovery from the anesthesia before a specimen was placed in an activity recorder.



Figs. 5-8.—5. Twenty-four hour locomotor activity rhythm of allatectomized *Romalea microptera* more active in the forenoon than at other times of day (type A). 6. Twenty-four hour locomotor activity rhythm of allatectomized *Romalea microptera* more active in the afternoon than at other times of day (type B). 7. Twenty-four hour locomotor activity rhythm of brainless *Romalea microptera* more active in the forenoon than at other times of day (type A). 8. Twenty-four hour locomotor activity rhythm of brainless *Romalea microptera* more active in the afternoon than at other times of day (type B).

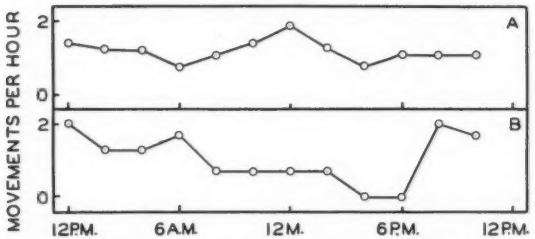


Fig. 9.—A, average 24-hour activity record of 14 *Romalea* that lacked a subesophageal ganglion; B, 24-hour activity record of three *Romalea* that lacked a subesophageal ganglion but with three subesophageal ganglia implanted into the abdomen of each.

The averaged results obtained with 14 *Romalea* whose subesophageal ganglion had been removed were shown in fig. 9A. As evident from the figure the operated specimens exhibited very little activity throughout the entire 24-hour day. The average number of movements per hour was 1.2. Furthermore, no indication of either type A or B activity rhythm was apparent from the data. The subesophageal ganglion was essential for the visible expression of the locomotor activity rhythm.

Harker (1956) demonstrated that headless *Periplaneta americana* did not exhibit an activity rhythm but that subesophageal ganglia implanted into headless *Periplaneta* evoked the expression of an activity rhythm. In view of the results of Harker three subesophageal ganglia were implanted into the abdominal cavity of each of three *Romalea* whose subesophageal ganglion had been removed previously. The following day the *Romalea* were placed in an activity recorder. As evident from the results obtained from the specimens with implanted subesophageal ganglia (fig. 9B), the implants neither increased the total activity nor induced an apparent locomotor activity rhythm. The average number of movements per hour of the specimens implanted with subesophageal ganglia was 1.1 as compared with 1.2 for specimens lacking a subesophageal ganglion that did not receive the implants.

DISCUSSION

The population of the grasshopper *Romalea microptera* consisted of approximately equal numbers of two types of individuals with respect to their 24-hour rhythms of locomotor activity and oxygen consumption. One group was more active during the forenoon than at other times of day (type A) and the other more active in the afternoon than at other times of day (type B). The rhythmical nature, A or B, of 115 different individuals was determined, of these 60 were type A and 55 type B.

Fingerman and Lago (1957) described two types of locomotor activity rhythms in the crawfish *Orconectes clypeatus*. Maximum spontaneous locomotor activity of intact *Orconectes* occurred about 6 A.M. in one group and 6 P.M. in the other group in contrast to 10 A.M. and 4 P.M. in intact *Romalea*. Furthermore, the rhythms of *Orconectes* tended to be bimodal with secondary maxima about 12 hours after the primary maxima, whereas bi-

modality was not consistent in the records of *Romalea*. The times of maximum activity of *Romalea* also differed from those reported for the other saltatory orthopterans that have been investigated, *Gryllus domesticus, G. assimilis,* and *Stenopelmatus* sp. by Lutz (1932). The latter species was most active about midnight, the others near 9 P.M.

The metabolic and locomotor activity rhythms must have been determined by the grasshoppers and were not an artifact due to the methods of recording activity and oxygen consumption. The experiments with *Orconectes* and *Romalea* were performed with the same apparatus and the same methods of analysis of data were used and yet the results with the two organisms were extremely different. In all probability if the apparatus had played a part in the expression of these rhythms, the results obtained with *Romalea* and *Orconectes* would have been quite similar.

Allatectomy had no apparent influence upon the expression of the activity rhythm whereas brain removal resulted in a slight decrease of over-all activity. Roeder (1953) reviewed the effects of removal of brain and subesophageal ganglion from several insects. Brain removal generally resulted in increased locomotor activity, because the brain contains a center of inhibition of locomotion, and decreased muscle tonus. Removal of the subesophageal ganglion generally resulted in complete cessation of locomotor activity. The lack of apparent increased locomotor activity of brainless *Romalea* may have been due to the method of recording activity. Because of the general decrease of muscle tonus associated with brain removal, the grasshoppers may not have been able to pull the recording levers as efficiently as intact specimens so that small movements failed to appear on the kymograph records.

The maxima of locomotor activity of intact type A and B grasshoppers occurred at the same hours as the maxima of the corresponding types of allatectomized *Romalea* but the maxima in the records of brainless grasshoppers shifted two to four hours earlier in the day. The brain, although not the seat of 24-hour rhythmicity in *Romalea,* may function to prevent drift of the maximum from the prescribed time set in intact specimens.

The seat of expression of 24-hour rhythmicity of spontaneous locomotor activity may be the subesophageal ganglion of *Romalea* just as shown by Harker (1956) for the cockroach *Periplaneta*. However, these results do not prove that the subesophageal ganglion of *Romalea* is the center of 24-hour rhythmicity but only that the center of rhythmicity of locomotor activity must operate through the subesophageal ganglion that exercises normal control over locomotion.

Romalea are normally found feeding in the field in the morning and afternoon but not during the middle of the day. Possibly type A specimens are those that feed in the morning and type B those that feed in the afternoon.

SUMMARY

Spontaneous locomotor activity and oxygen consumption of the grasshopper *Romalea microptera* were recorded continuously for 24-hour periods.

Analysis of the data revealed 24-hour rhythms of both spontaneous locomotor activity and metabolic rate.

The population consisted of two types of individuals. One type exhibited maxima of locomotor activity and metabolic rate in the forenoon. The

second type exhibited maxima of locomotor activity and metabolic rate in the afternoon. The average interval between the maxima of the two types was seven hours in intact *Romalea*.

Allatectomized and brainless *Romalea* also exhibited both types of locomotor activity rhythm.

Romalea whose subesophageal ganglion had been removed showed no overt rhythm. Implanted subesophageal ganglia failed to induce an overt rhythm in individuals whose subesophageal ganglion had been removed.

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Studies on the Trematode Family Dicrocoeliidae. I. The Genera Brachycoelium (Dujardin, 1845) and Leptophallus Luhe, 1909, (Brachycoeliinae)

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Although the taxonomy of the trematode family Dicrocoeliidae Odhner, 1910, has been studied to some extent, and two monographs have appeared, Travassos (1944) and Skrjabin (1952), both of these works unfortunately excluded some of the American forms. Also there were some disagreements as to the method of classification within the family. The subfamily Brachycoeliinae was omitted; hence, several important genera belonging to this group were left out. This series of taxonomic and morphological studies on this extremely large family is a re-evaluation of the taxonomy of this group, and it will serve as a check-list of the known species. The author has recorded and briefly described the members of the family, giving only the very essential characteristics. Because of the large number of genera and species represented in the Dicrocoeliidae, the complete monograph is being divided into several parts; the first of these, represented by this paper, deals with the genera *Brachycoelium* and *Leptophallus* of the subfamily Brachycoeliinae.

Acknowledgment.—The author is indebted to Dr. Allen McIntosh of the Animal Disease and Parasite Research Branch of the Agricultural Research Center, Bethesda, Maryland, through whose courtesy he had the opportunity to examine the available type and paratype specimens of the various species deposited in the United States National Museum. Many of the materials also used in this series of studies were collected from various localities, while others were loaned to the author by Dr. Bruce D. Reynolds of the University of Virginia. Drawings of the various species are included since they provide the information as to the location and arrangement of internal organs, these characteristics having been deleted from the individual descriptions for the sake of brevity.

The author wishes to thank Dr. B. D. Reynolds for his encouragement and valuable advice during the course of this study and Mr. Robert Gillespie, University of Virginia, for aiding in the collecting of some of the hosts.

The number of subfamilies assigned to the family Dicrocoeliidae Odhner, 1910, is uncertain. Johnston (1927) erected Tandanicolae around the type *Tandanicola bancrofti*, but it has not been accepted to any extent. Baer (1924) erected Cymatocarpinae around *Cymatocarpus* Looss, 1899; Dollfus (1929) erected Mesocoeliinae around the genus *Mesocoelium* Odhner, 1911, but these again have not been accepted by most workers. Dollfus (1937) erected Orchidasmatinae around *Orchidasma* Looss, 1900; although this subfamily was used by Hughes *et al.* (1942) in their systematic listing of trematodes of reptiles, it is still not in common usage. This present series of papers will serve to further strengthen the deletion of the above mentioned subfamilies

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from future literature. Travassos (1944) erected Infidinae which Skrjabin (1952) included in his monograph of the family along with Dicrocoeliinae Looss, 1899, but excluded Brachycoeliinae Looss, 1899, which Johnston (1912) had elevated to the rank of family, Brachycoeliidae. The validity of this move has been debated by several workers led by Fuhrmann (1928) who retains the subfamily rank for this group. Faust (1929) did include Brachycoeliidae as a family in his superfamily Dicrocoelioidea, but the author agrees with Fuhrmann in retaining Brachycoeliinae as a subfamily under Dicrocoeliidae until additional evidences can indicate differently. Patten (1952), in agreement with Dawes (1946), stated that there are two subfamilies in Dicrocoeliidae, these being Brachycoeliinae and Dicrocoeliinae; the first contains parasitic forms in amphibians and reptiles, and the latter contains forms parasitic in birds and mammals. Upon reviewing the diagnostic descriptions of the various subfamilies, the author concluded that there are three valid subfamilies in Dicrocoeliidae, these being Brachycoeliinae, Dicrocoeliinae, and Infidinae. The specific descriptions of these subfamilies will be given in the sections devoted to them.

Subfamily BRACHYCOELIINAE Looss, 1899

This series of studies indicates that there are eight genera included in the subfamily Brachycoeliinae, these being: *Brachycoelium* (Dujardin, 1854) Stiles and Hassal, 1898, *Leptophallus* Lühe, 1909, *Glypthelmins* Stafford, 1905, *Margeana* Cort, 1919, [considered in synonymy with *Glypthelmins* by Miller (1930)], *Mesocoelium* Odhner, 1911, *Pintneria* Poche, 1907, *Orchidasma* Braun, 1901, and *Cymatocarpus* Braun, 1901. The members of this subfamily may be characterized as follows:

Delicate distomes with spinous and aspinous cuticula; body shape ranging from elongate to subspherical; suckers subequal with acetabulum usually in anterior half of body; intestinal ceca ranging from extremely short in *Brachycoelium* to very long in *Glypthemins* and *Orchidasma;* ovary usually smaller than testes and anterior or posterior to them; uterus filling posterior portion of body, below the level of testes, with ascending and descending limbs; eggs small, thick-shelled, operculated; vitellaria follicular; excretory bladder Y- or modified Y-shaped. The latter is more common (often referred to as of the I-type). Parasitic in intestines of amphibians and reptiles.

Genus BRACHYCOELIUM (Dujardin, 1845) Stiles and Hassall, 1898

In the literature, 14 species belonging to this genus have been described. Rankin (1938) reduced all the American species to synonymy with *B. salamandrae* (Frolich, 1789) [= *B. crassicolle* (Rudolphi, 1890)], since in his studies he considered that the criteria used by others in separating the species were invalid. The present author has studied over 300 specimens of *Brachycoelium* spp. collected in Albemarle and Giles counties in Virginia during 1955-56, and has compared these with the type and paratype specimens in the U. S. National Museum, and he finds that he disagrees with Rankin in the latter's proposal to relegate all the forms to synonymy with *B. salamandrae.* This careful approach in re-evaluating the species of *Brachycoelium* is shared by Parker (1941) who stated that he collected specimens in Tennessee and Georgia which distinctly conformed to the diagnostic characteristics of some particular species and not to others. These recent studies by the author have all been morphological; however, life history studies are presently

being carried out to further clarify the species problem in this genus. This paper serves to catalog the species which the author considers valid, and the reasons for validity are considered.

The generic characteristics for *Brachycoelium* are re-written in the light of recent studies to read as follows:

Body elongate to subspherical, slightly dorso-ventrally flattened; cuticle partially spinous in the living state; suckers subequal, acetabulum anterior to equator of body; intestinal ceca short, ending short of level of acetabulum; cirrus pouch small, enclosing seminal vesicle and cirrus, mainly in front of acetabulum, opening in the median plane; testes close behind acetabulum, lateral or obliquely tandem; ovary in front of testes; vitellaria in anterior part of body, lateral to ceca in some, filling anterior of body in region of ceca in others; uterus with ascending and descending limbs, abundantly folded, the folds filling most of space anterior to testes; oötype, Mehlis' gland, seminal receptacle and Laurer's canal present; excretory vesicle modified Y-shaped (I-type), with short cornua; flame-cell pattern, according to Byrd (1937) of 2x3x6 type. Parasites in intestines of amphibians and reptiles.

Type species.—*B. salamandrae* (Frolich, 1789).

BRACHYCOELIUM SALAMANDRAE (Frolich, 1789)

Plate 1, fig. 1

Syn. *Fasciola salamandrae* Frolich, 1789; *Distoma salamandrae* Zeder, 1803; *Distoma crassicolle* Rudolphi, 1809; *Distomum flavocinctum* Linstow, 1879; *Brachycoelium crassicolle* (Frolich, 1789) Looss, 1899; *Lecithodendrium crassicolle* (Frolich, 1789) Stossich, 1799; *Brachycoelium hospitale* Stafford, 1903.

Diagnosis.—Elongate, 2-5 mm long; 0.8-1.2 mm wide. Cuticle more spinous in anterior region. Ventral sucker 0.20-0.26 mm x 0.26-0.31 mm. Prepharynx, pharynx, and esophagus present. Ceca short. Testes rounded, side by side, behind tips of ceca and acetabulum. Ovary in front of left testis, behind acetabulum. Vitellaria anterior, on marginal side of ceca. Eggs light brown, 0.045-0.05 mm x 0.032-0.036 mm.

Hosts.—Common newt, common frog, common toad, salamander.

Type locality.—Europe.

This is the first species of *Brachycoelium* to be described. Stafford (1900) described *Distoma hospitale* (Plate 3, fig. 3), and later (1903) placed it in the genus *Brachycoelium*. This worm was first reported from *Triturus viridescens* and *Plethodon erythronotus;* Harwood (1932) reported it from *Rana sphenocephala,* and Byrd (1937) reported it from *Ambystoma opacum* and *Plethodon glutinosus*. The author has collected approximately 50 specimens from *Plethodon glutinosus* and *P. cinereus* at Mountain Lake, Virginia. He has also studied specimen No. 30870 USNM collected by P. D. Harwood. Upon critical examination of both living and mounted specimens, the author agrees with Rankin (1938) that *B. hospitale* is identical with the type species. The general body outline, the body and internal organ dimensions, are all within the same ranges and in the same positions. The distribution and positions of the vitellaria are identical. The acetabulum of *B. hospitale* (0.144 x 0.138 mm) is slightly smaller than that of *B. salamandrae* (0.26-0.31 x 0.20-0.26 mm), but this slight variation in the sizes of the acetabulum was noted as a common phenomenon even within *B. hospitale,* and it is probably due to the state of contraction of the musculature. Stafford, in his description, appeared to have been influenced by the geographical location, since this worm was the first to be described in North America. In regard to this species, the author is placing it in synonymy with the type, *B. salamandrae.*

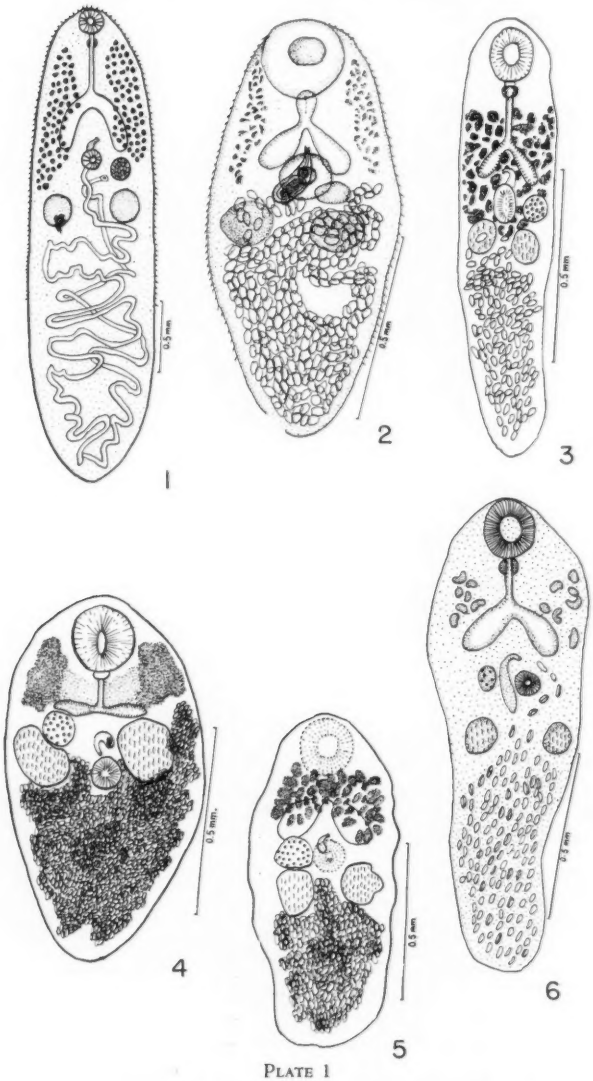

PLATE 1

Figs. 1-6.—1. *Brachycoelium salamandrae* (Frolich, 1789). Ventral view. (After Lühe, 1909). 2. *B. obesum* Nicoll, 1914. Ventral view. (After Nicoll, 1914). 3. *B. storeriae* Harwood, 1932. Ventral view. (After Harwood, 1932). 4. *B. daviesi* Harwood, 1932. Ventral view. (After Harwood, 1932). 5. *B. meridionalis* Harwood, 1932. Dorsal view. (After Harwood, 1932). 6. *B. trituri* Holl, 1928. Ventral view. (After Holl, 1928).

BRACHYCOELIUM OBESUM Nicoll, 1914

Plate 1, fig. 2

Syn. *B. ovale* Byrd, 1937.

Diagnosis.—Oval distomes, more rounded anteriorly. 0.75-1.5 mm long, 0.4-0.65 mm wide. Cuticle spinous. Anterior sucker, 0.17-0.25 mm in diameter; acetabulum, near the middle of the body, 0.11-0.15 mm in diameter. No prepharynx reported, pharynx and short esophagus present. Testes oval, approximately twice the size of ovary, situated on the same level. Ovary transversely oblong, 0.13 x 0.07 mm, is partially overlapped by acetabulum. Conspicuous cirrus sac very large, extending across the acetabulum. Vitellaria lateral to ceca, from margins of anterior sucker to level of acetabulum. Eggs, 0.05-0.052 x 0.034-0.036 mm.

Host.—*Contia aestiva.*

Type locality.—London Zoological Gardens (probably imported with the host).

Although Rankin (1938) considers this species to be identical with *B. salamandrae,* the author feels that unless life-history studies can show differently *B. obesum* is to be considered a valid species, inasmuch as all of Nicoll's specimens were significantly smaller than the given dimensions of *B. salamandrae,* and the extremely large cirrus pouch serves as an outstanding specific difference. The validity of this species was also championed by Parker (1941) who distinctly separated *B. obesum* from others in the genus in his collections from *Desmognathus f. fuscus, Plethodon glutinosus,* and *Eurycea bislineata cirrigera* in Tennessee and Georgia. The author was able to recover flukes of this species from *Plethodon cinerus* and *P. glutinosus* from Virginia, and the life history of *B. obesum* has been worked out and will be reported in a subsequent paper. He did note that some of the specimens had slightly larger vitelline follicles, and these were slightly more posterior in position.

Byrd (1937) described *Brachycoelium ovale* (Plate 2, fig. 3) from *Leiolopisma laterale* from Georgia, and Parker (1941) found representatives of this species from *Desmognathus f. fuscus* and *Plethodon glutinosus* at Rome, Georgia. The type specimen No. 9028, USNM, was studied in some detail. This fluke closely resembles *B. obesum,* since the pattern of the distribution of the vitellaria, which are lateral to the ceca, and the median positions of the testes, on each side of the acetabulum, are common to both species. Byrd, in the original description, stated that *B. ovale* had smaller body and sucker sizes than *B. obesum;* however, this was not found to be the case since the oral sucker of *B. ovale* has a diameter of 0.184 mm, while Nicoll (1914) reported this diameter to be 0.17-0.25 mm in *B. obesum.* The acetabulum of *B. ovale* is 0.09 mm in diameter, while those of *B. obesum* range from 0.11-0.15 mm, an insignificant difference, especially for suckers. The body size of *B. ovale* is 0.90 x 0.61 mm, and that of *B. obesum* is 0.75-1.5 mm x 0.4-0.65 mm, indicating no difference in body sizes. Basing the decision on the great similarity of the specific differences, the author concludes that *B. ovale* is to be reduced to synonymy with *B. obesum.*

BRACHYCOELIUM STORERIAE Harwood, 1932

Plate 1, fig. 3

Syn. *B. dorsale* Byrd, 1937.

Diagnosis.—Body elongate, 1.9 mm long, 0.25 mm wide. Fine cuticular spines in region of oral sucker, disappear before reaching middle of body. Oral sucker 0.140 mm

in diameter; acetabulum 0.084 x 0.100 mm. Prepharynx, pharynx and long esophagus (0.126 mm) present. Ovary spherical, 0.070 mm in diameter. Vitellaria extensively developed, occupying area bordered by lateral body walls, from just below the pharynx to level of testes and dorsally filling the medial portion of the body. Testes 0.080 x 0.047 mm. Eggs, 50 x 34 microns.

Host.—*Storeria dekayi.*

Type locality.—Houston, Texas.

This is the first species of *Brachycoelium* to be described which possesses vitellaria which fill the entire dorsal portion of the body within the given anterior and posterior boundaries. This extensively developed vitellaria easily separates it from *B. salamandrae* and *B. obesum*. Rankin (1938) again claims *B. storeriae* to be identical with the type species, but of the 150 mature specimens of *B. salamandrae* which the author has studied, in none was the vitellaria as extensive, or filling the medio-dorsal region of the body, as in *B. storeriae*. The type specimen for this species, USNM No. 30873, was studied, and the constitution of the vitellaria must be considered a valid specific characteristic. Parker (1941) was able to identify representatives of this species from *Ambystoma opacum* from Reelfoot Lake, Tennessee, and from *Pseudotriton r. ruber* and *Opheodrys aestivus* from Athens, Georgia. The author collected four flukes of this species from *Plethodon cinereus* at Mountain Lake, Virginia.

Byrd (1937) described *Brachycoelium dorsale* (Plate 2, fig. 5) from the small intestines of *Ambystoma opacum* from Pearl River, Louisiana. The author was able to study the type specimen, USNM No. 9029. This species appears to be identical with *B. storeriae*. Byrd recognized the great similarity, but created the new species because of "the extent and configuration of the vitellaria, the larger suckers, the larger ovary and testes, and the transverse looping of the uterus." From the description of *B. storeriae* and the original plate drawn from the type, it is quite simple to see that the type specimen was greatly contracted laterally which probably accounts for its narrower appearance and the drawn out appearance of the vitellaria which normally, as in the author's specimens, would be identical with that of *B. dorsale*. The anterior sucker of *B. storeriae* is 0.14 mm in diameter, and that of *B. dorsale* measures 0.15 mm, certainly an insignificant difference for suckers; the acetabulum of *B. dorsale* is 0.105 x 0.122 mm while that of *B. storeriae* is 0.11-0.15 mm in diameter, again the slight difference can be attributed to the degree of contraction. The ovary and testes of both species are of the same size, with a negligible variation of 0.03 mm. The author does not feel there is sufficient difference between these two species to warrant the validation of *B. dorsale* which is hereby reduced to synonymy with the older *B. storeriae*.

BRACHYCOELIUM DAVIESI Harwood, 1932

Plate 1, fig. 4

Diagnosis.—Body oval, 0.65-0.95 mm long, 0.3-0.55 mm wide. Fine cuticular spines at anterior end. Oral sucker 0.13-0.23 mm in diameter; acetabulum 0.125 mm in diameter. Prepharynx not reported, pharynx and short esophagus (0.03 mm) present. Ovary circular 0.1 mm in diameter. Vitellaria well developed, heaviest lateral to esophagus, with one band joining dorso-medially, bordered by pharynx and ceca. Eggs 24-31 microns x 40-42 microns.

Hosts.—Leiolopisma laterale, Pseudacris triseriata, Hyla cinerea, Ambystoma microstomum.

Type locality.—Houston, Texas.

The paratype, USNM No. 30877 was carefully studied. At first appearance, it resembled *B. storeriae* inasmuch as the vitellaria are well developed and joining along the dorso-medial line, although the follicles were not distinct and independent as in *B. storeriae*. *B. daviesi* is not as elongated as *B. storeriae*, and the testes maintain a much more anterior position, being partially anterior to the level of the acetabulum. The prepharynx is absent in *B. daviesi*, while it is conspicuously present in *B. storeriae*. Other minor differences in body and internal organ dimensions have proven to be unreliable in separating the species.

BRACHYCOELIUM MERIDIONALIS Harwood, 1932

Plate 1, fig. 5

Diagnosis.—Body irregularly oval, 0.8-0.95 mm long, 0.3-0.4 mm wide. Cuticle spinous. Anterior sucker 0.145 mm in diameter; acetabulum 0.125-0.138 mm in diameter. Prepharynx present, the latter being twice as long as the former. Testes slightly irregular, 0.105-0.115 mm in diameter. Globular ovary, 0.076-0.084 mm in diameter. Vitellaria lie between the levels of the middle of esophagus and ends of ceca. Eggs 29 x 42 microns.

Host.—Triturus meridionalis.

Type locality.—Houston, Texas.

The slide marked USNM No. 30875 revealed two paratypes of this species. At first glance, these resembled *B. storeriae* and *B. daviesi*, since the vitellaria, like in the two closely related forms, are connected dorso-medially; however, it can be separated from the mentioned species by its extremely short esophagus which is only twice the length of the pharynx. Again, it can be distinguished from *B. daviesi* by the position of the testes which are completely posterior to the level of the acetabulum, rather than partially anterior as in *B. daviesi*.

BRACHYCOELIUM TRITURI Holl, 1928

Plate 1, fig. 6

Diagnosis.—Elongate body measuring 1.4 mm long and 0.442 mm wide. Subterminal oral sucker, 0.167 mm in diameter. Small acetabulum near middle of body, 0.836 mm in diameter. Inconspicuous prepharynx seen, although not reported by Holl. Pharynx and long narrow esophagus present. Left testis is 0.095 x 0.076 mm, right testis 0.084 x 0.076 mm, both situated on the same plane posterior to acetabulum. Ovary 0.091 x 0.053 mm, situated on right of acetabulum. Cirrus sac, 0.134 mm long x 0.061 mm wide, is also on the right of the ventral sucker. Vitelline follicles large, sparse, 6-8 on each side, situated dorsal to esophagus and intestinal ceca.

Host.—Triturus viridescens.

Type locality.—Lakeview, North Carolina.

The type specimen, USNM No. 7994, was studied, also many specimens collected in Charlottesville, Va., where this parasite is commonly found in *Triturus viridescens*. This species, although questionable, must be considered valid until further evidence can be provided

to reduce it into synonymy with one of the older species. The main specific characteristic appears to be the anterio-lateral position of the vitellaria which do not extend beyond the tips of the ceca. Byrd (1937) was able to identify representatives of this species from *Rana sphenocephala* from Harvey, Louisiana, *Pseudacris occidentalis* from Kenner, Louisiana, and *Desmognathus f. fuscus* from Athens, Georgia. However, Byrd reported slightly more extensive vitellaria. *B. trituri* resembles *B. salamandrae* and *B. obesum,* although it can be separated from the former by its less extensive vitellaria and a much larger and more conspicuous cirrus sac; it differs from the latter by the presence of a longer esophagus and narrower cirrus sac. In his original description, Holl did not mention the presence of a prepharynx which the author distinctly saw on the type specimen; the presence of this is of some diagnostic importance. Holl described and pictured the cirrus sac lying between the ovary and acetabulum; however, the paratype showed a wider cirrus sac which was partially covered by the acetabulum, measuring 0.100 x 0.041 mm and containing a bilobed seminal vesicle and a cirrus.

BRACHYCOELIUM MESORCHIUM Byrd, 1937

Plate 2, fig. 1

Diagnosis.—Body elongate oval, 1.3-2.7 mm long, 0.42-0.69 mm wide. Cuticle spinous to level of testes. Anterior sucker 0.165 mm in diameter; acetabulum 0.166 mm in diameter. Testes distinctly on two levels, anterior one more obliquely lateral to ovary; right testis 0.112 x 0.143 mm, left testis 0.104 x 0.153 mm. Oval ovary, 0.096 x 0.14 mm. Prepharynx, pharynx and esophagus present. Uterine loops strongly coiled. Vitellaria composed of rather large follicles, tending to form 2 or 3 clusters in anterior portion of body, extending posteriorly to level of posterior margin of acetabulum. Eggs 27-33 microns x 45-52 microns.

Host.—Desmognathus f. fuscus.

Type locality.—Athens, Georgia.

Thirty specimens identified as *B. mesorchium* were obtained from the same host in Giles and Albemarle Counties, Virginia. In addition to these, the type, USNM No. 9031, was studied. Although Byrd (1937) claimed that this species can be distinguished from the other by its nearly equal suckers, the medial position of testes and ovary, the configuration of the vitellaria, and the pattern of the uterine coils, the author tends to agree with Rankin (1938) that these differences are not sufficient in separating it from the other species. Unlike Rankin, the author feels that the size, shape, and position of the testes are significant as specific characteristics. Although the laterally situated vitellaria separates it from *B. storeriae, B. daviesi,* and *B. meridionalis,* it does not differentiate it from *B. salamandrae, B. obesum,* and *B. trituri.* However, the testes of *B. mesorchium* are larger and more spindle-shaped than those found in the last three species mentioned, and they are arranged so that the left testis is posterior to the right, a pattern not present in any of the other three closely related species.

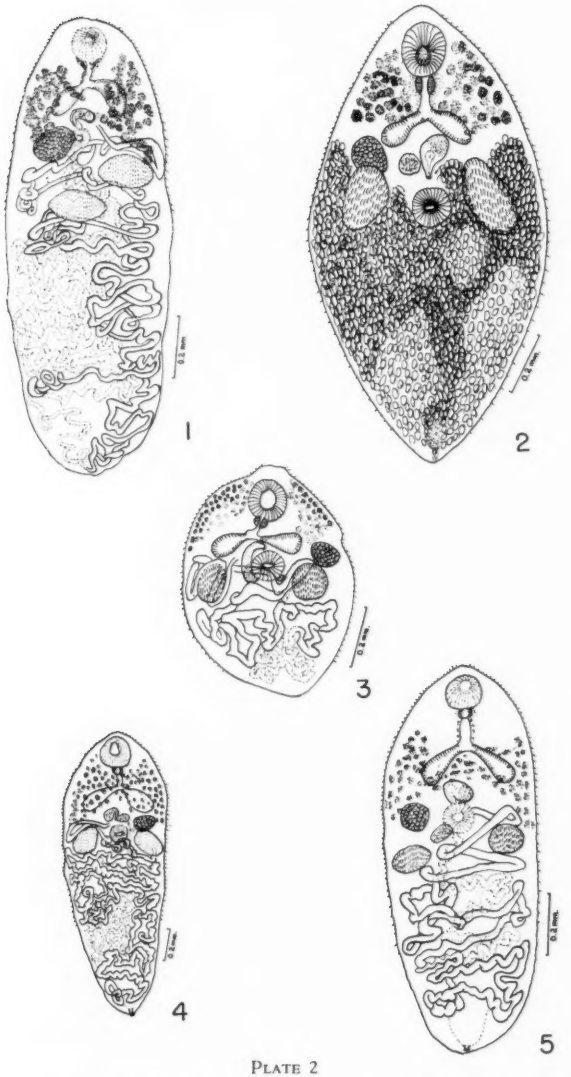

PLATE 2

Figs. 1-5.—1. *Brachycoelium mesorchium* Byrd, 1937. Dorsal view. (After Byrd, 1937). 2. *B. georgianium* Byrd, 1937. Ventral view. (After Byrd, 1937). 3. *B. obesum* Nicoll, 1914 (=*B. ovale* Byrd, 1937). Ventral view. (After Byrd, 1937). 4. *B. louisianae* Byrd, 1937. Dorsal view. (After Byrd, 1937). 5. *B. storeriae* Harwood, 1932 (=*B. dorsale* Byrd, 1937). Dorsal view.

BRACHYCOELIUM GEORGIANIUM Byrd, 1937

Plate 2, fig. 2

Diagnosis.—Body spindle-shaped, 1.326 mm long, 0.8 mm wide. Cuticle spinous for entire length, except extreme posterior end. Anterior sucker 0.206 x 0.191 mm; acetabulum one-half the size of anterior sucker. Testes at approximately the same level, lateral to acetabulum; right testis, 0.223 x 0.164 mm; left testis 0.241 x 0.166 mm. Ovary subspherical, 0.046 x 0.14 mm. Prepharynx, pharynx and esophagus present. Vitellaria lateral to ceca, seldom overlapping ceca except marginally, extending between caudal end of ceca to equatorial plane of oral sucker. Eggs, 27-33 microns x 42-45 microns.

Host.—Rana sphenocephala.

Type locality.—Athens, Georgia.

The type specimen, USNM No. 9030, was studied. The laterally situated vitellaria easily separates this species from *B. storeriae, B. daviesi,* and *B. meridionalis,* but this characteristic does not differentiate it from *B. salamandrae, B. obesum, B. trituri,* and *B. mesorchium,* since in these the vitellaria are also completely lateral in position. Byrd (1937) stated that *B. georgianium* is most closely related to *B. mesorchium,* although upon more careful comparison the author feels that it is just as similar to *B. obesum.* The size and position of the testes appear to be the main diagnostic characteristic, since these organs are slightly larger in *B. georgianium* than those of the closely related species, and they are situated on the same level as the acetabulum, a phenomenon not occurring in the others.

BRACHYCOELIUM LOUISIANAE Byrd, 1937

Plate 2, fig. 4

Diagnosis.—Body elongate, 2.04-3.1 mm long x 0.72 mm wide. Cuticle spinous. Oral sucker 0.20 mm in diameter; acetabulum 0.134 mm in diameter. Prepharynx, pharynx, and esophagus (0.17 mm long) present. Ovary transversely oval, 0.128 x 0.149 mm situated close behind the cecum on left or right side and anterior to acetabulum. Vitellaria dispersed superficially just under dorsal surface, continuous from side to side, extending from level of oral sucker to level of ovary, overlapping the intestinal ceca. Testes on same level as acetabulum on each side of it; right testis 0.233 x 0.227 mm, left testis 0.251 x 0.240 mm. Eggs 30 x 45 microns.

Host.—Ambystoma opacum.

Type locality.—Pearl River, Louisiana.

Besides the type specimen, USNM No. 9027, 21 representatives of this species were used; these additional specimens were recovered from *Plethodon cinereus.* The pattern of the vitellaria, being connected along the median plane, separates *B. louisianae* from *B. salamandrae, B. obesum, B. trituri, B. mesorchium,* and *B. georgianium.* The anterior position of its testes, at the level of the acetabulum, separates *B. louisianae* from *B. storeriae* and *B. meridionalis.* It is most similar to *B. daviesi* from which it cannot be separated by the above mentioned major characteristics; however, *B. daviesi* (0.65-0.95 x 0.3-0.55 mm) is much smaller than *B. louisianae* (2.04-3.1 x 0.72 mm) in body size, and also all internal organs of *B. daviesi* are approximately twice as small as in *B. louisianae,* despite the fact that both type specimens are fully mature and filled with embryonated eggs. Furthermore, the vitelline follicles of *B. louisianae* cover the entire digestive tract dorsally, while in *B. daviesi* only the esophagus is covered dorsally by the vitellaria.

Brachycoelium elongatum n. sp.

Plate 3, fig. 4

The following description is based on eight specimens of the new species. Four of these were recovered from the intestines of the black-bellied salamander, *Desmognathus q. quadrimaculatus* (Holbrook) by Dr. B. D. Reynolds in August, 1939, at Mountain Lake, Virginia; three specimens from the seal salamander, *Desmognathus phoca* (Matthes) by Dr. Reynolds at the same time and same geographic locality; one specimen was recovered from the small intestine of *Plethodon glutinosus* by the author in July, 1955, at the same locality.

The specimens were fixed under slight pressure with Carnoy's (6:1:1) and stained with Harris' Alum Hematoxylin. All of the older specimens had to be restained.

Diagnosis.—(All measurements given in millimeters.) Body slightly dorso-ventrally flattened, narrow and long, 2.24 long (maximum, 3.10; minimum, 1.72), 0.339 wide (maximum, 0.389; minimum, 0.286); the ratio of length to width approximates 11:2. Cuticle spinous in anterior portion of body, becoming less spinous posteriorly, spines ending at posterior level of ovary. Anterior sucker subterminal, 0.127 (maximum, 0.15; minimum, 0.111) by 0.12 (maximum, 0.14; minimum, 0.101). Extremely short prepharynx, invisible in some specimens, 0.002 in mean length; muscular pharynx averaging 0.045 in diameter; long esophagus 0.164 in mean length (maximum, 0.228; minimum, 0.107), bifurcating slightly anterior to midpoint between pharynx and acetabulum. Intestinal ceca elongately bulbous, averaging 0.274 long, parallel to each other, ending in front of level of anterior margin of acetabulum. Subcircular acetabulum, smaller than anterior sucker, situated in anterior half of body, posterior to termination of right cecum, averaging 0.082 x 0.078. Two irregularly oval testes situated in mid-section of body; in all cases left testis posterior to right; left testis 0.159 (maximum, 0.169; minimum, 0.130) by 0.124 (maximum, 0.156; minimum, 0.094), right testis 0.15 (maximum, 0.169; minimum, 0.127) by 0.123 (maximum, 0.146; minimum, 0.098). Respective efferent duct arises from anterior border of each testis and proceeds anteriorly to just posterior to cirrus where the two join to form the short common vas deferens which enters the cirrus sac. Cirrus sac, with average length of 0.132 and average width of 0.042, contains a bilobed seminal vesicle which measures 0.071-0.059 long and 0.049-0.024 wide. Cirrus situated anterior to seminal vesicle averages 0.086 long; it opens in area of genital pore which is immediately anterior to acetabulum. Subspherical ovary, 0.1 (maximum, 0.12; minimum, 0.065) long and 0.088 (maximum, 0.114; minimum, 0.052) wide, situated to the left and posterior to the acetabulum. A short oviduct arises from the medio-lateral margin of ovary and enters into oval oötype; oötype measures 0.016 x 0.013. Amorphic Mehlis' gland, situated immediately posterior to oötype. Laurer's canal present, arising from dorsal surface of oötype. Large compressed seminal receptacle, lying between ovary and cirrus sac, averaging 0.076 long and 0.051 wide. Long transversely convoluted uterine tract, with ascending and descending loops, filled with thick-shelled yellowish-brown eggs, 0.056-0.042 long, 0.033-0.029 wide. Vitellaria follicular, lateral to ceca, extending anteriorly from level of mid-region of ceca posteriorly to level of ovary, joining in area of acetabulum and ovary.

Hosts.—*Desmognathus phoca, Desmognathus q. quadrimaculatus, Plethodon glutinosus.*

Habitat.—Intestine.

Type locality.—Mountain Lake, Giles County, Virginia.

Type specimen.—USNM Helm. Coll. No. 55608.

Paratype.—USNM Helm. Coll. No. 55607.

The main characteristic which separates this new species from the earlier forms is its striking body length. The body of *B. elongatum* is approximately seven times as long as its width. The second striking characteristic which

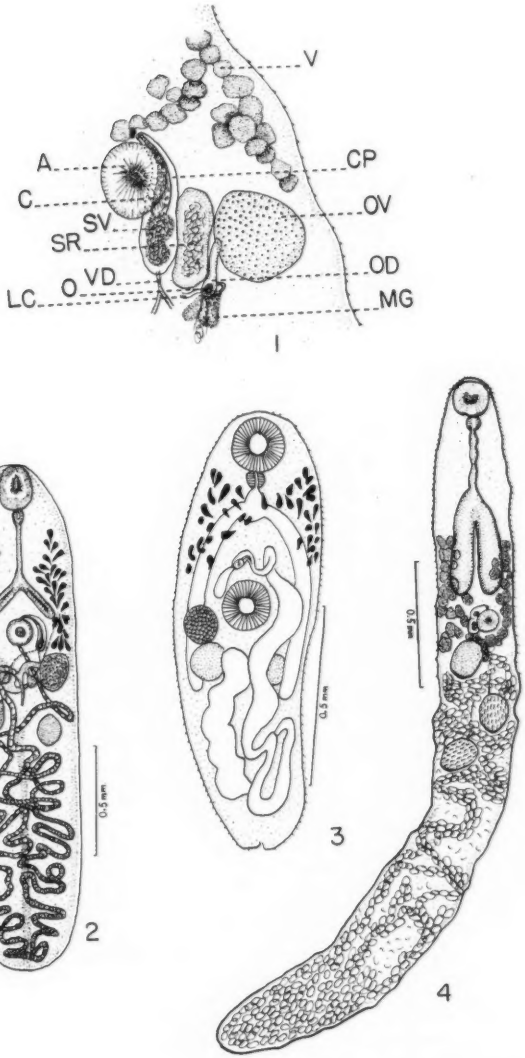

PLATE 3

Figs. 1-4.—1. *Brachycoelium elongatum* n. sp., showing female reproductive system and cirrus sac. 2. *B. salamandrae* (Frolich, 1789) (= *B. hospitale* Stafford, 1903). Ventral view. (After Stafford, 1905). 3. *Leptophallus nigrovenosus* (Bellingham, 1844) Lühe, 1909. 4. *B. elongatum* n. sp. Dorsal view.

might be used in differentiating it is the arrangement of the vitellaria. Their anterior limit is the midregion of the ceca; their posterior, the anterior testis. At the posterior level the follicles join dorso-medially in the area just above the anterior testis. These two diagnostic differences easily separate *B. elongatum* from the other species of the genus.

DISCUSSION

Ingles (1936) described *Brachycoelium lynchi* from *Rana aurora*. The slide, including the type, designated as USNM No. 8933, held 17 specimens of this species. A critical study of these specimens revealed that Rankin (1938) was correct in transferring this species to another genus; however, the author doubts whether *Lecithodendrium* is the correct one, since from his past experience with this genus, although recognizing the similarity, he is doubtful as to whether *B. lynchi* belongs in this genus, since the characteristic prostate mass of *Lecithodendrium* was not seen in any of the specimens. However, until more work can be done, no change is proposed at this time.

This study of *Brachycoelium* revealed that there are ten valid species including *B. elongatum* belonging to this genus. The paper also points out that some of the characteristics, such as ratio of suckers, position of suckers, size of ceca, and dimension of bodies, used up to now in separating the species, are too flexible to be of any value. The work of Cheng (1956) with *Acanthatrium* (Lecithodendriidae), pointed out a similar situation where sucker and body dimensions, unless radically different, were not reliable in separating the species of *Acanthatrium*. In *Brachycoelium*, the author considers the degree of development and distribution of the vitellaria, and the shape and positions of the testes to be the main diagnostic characteristics.

The following key to the valid species of *Brachycoelium* is based on our present knowledge of the genus, which is entirely morphological. The author realizes that current life-cycle studies, which are being carried on at this laboratory, may reveal the invalidity or validity of other species in the future.

KEY TO THE GENUS BRACHYCOELIUM

1. Vitellaria lateral to intestinal ceca; not joining on dorso-medial plane.
   - A. Testes situated lateral to and on same level as acetabulum ..... *B. georgianium* Byrd, 1937.
   - B. Testes situated posterior to level of acetabulum.
     - a. Testes situated one posterior to the other ..... *B. mesorchium* Byrd, 1937.
     - b. Esophagus inconspicuous and short ..... *B. obesum* Nicoll, 1914.
     - c. Vitellaria extending posteriorly beyond intestinal ceca ..... *B. salamandrae* (Frolich, 1789).
     - d. Vitellaria not extending beyond intestinal ceca ..... *B. trituri* Holl, 1928.
2. Vitellaria lateral to ceca and also joining on dorso-medial plane.
   - A. Testes on same level as acetabulum.
     - a. Body 0.65-0.95 mm long; vitellaria situated completely anterior to ceca ..... *B. daviesi* Harwood, 1932.
     - b. Body 2.04-3.1 mm long; vitellaria extending past tips of ceca ..... *B. louisianae* Byrd, 1937.
   - B. Testes situated posterior to level of acetabulum.
     - a. Esophagus long and slender.
       - i. Body approximately 7 times longer than wide; vitellaria joining only at the level of acetabulum ..... *B. elongatum* n. sp.

ii. Vitellaria joining dorso-medially all along the extent of the follicles extending to level of acetabulum ..... *B. storeriae* Harwood, 1932.
b. Esophagus short and inconspicuous; vitellaria not extending to level of acetabulum ..... *B. meridionalis* Harwood, 1932.

Genus LEPTOPHALLUS Luhe, 1909

Byrd (1937) did not list this genus in Brachycoeliinae; however, Hughes *et al.* (1941) and Dawes (1946) considered it a member of this subfamily. The author definitely feels that *Leptophallus* belongs here since it completely subscribes to the diagnostic characteristics of the subfamily as given earlier in this paper. The body shape and size, and the arrangement of the internal organs all closely approximate that of *Brachycoelium*. There is only one species recorded in the literature, and that is the type, *L. nigrovenosus* (Bellingham, 1844). The diagnosis for the genus is as follows:

Elongate oval distomes with slightly flattened bodies; cuticle spinous; powerful anterior sucker and acetabulum, both in anterior one-half of body; bifurcation of intestine well in front of acetabulum; intestinal ceca fairly long, reaching level of posterior margin of testes; genital pore near median, in front of acetabulum; cirrus pouch with large seminal vesicle and cirrus present; ovary in front of testes. Vitellaria confined to region between pharynx and acetabulum; uterus with ascending and descending limbs. Parasites of reptiles.

Type species.—Leptophallus nigrovenosus (Bellingham, 1844) Lühe, 1909.

LEPTOPHALLUS NIGROVENOSUS

Plate 3, fig. 3

Syn. *Distomum nigrovenosum* Bellingham, 1844; *Distoma signatum* Dujardin, 1845; *Distoma nigrovenosum natricis torquatae* Diesing, 1855; *Lecithodendrium nigrovenosum* (Bellingham, 1844) Looss, 1902; *Caudorchis signatum* (Dujardin) Talbot, 1934.

Diagnosis.—Body elongate oval, 1.1-1.8 mm long, 0.4-0.43 mm wide; cuticle completely spinous. Anterior sucker 0.21-0.26 mm in diameter; acetabulum 0.18-0.22 mm in diameter. Prepharynx absent, pharynx and short esophagus present. Ceca reaching slightly past level of posterior borders of testes. Vitellaria of large pyriform follicles, lateral to ceca, but overlapping marginally, between pharynx and acetabulum. Eggs 35-38 x 19-21 microns.

Hosts.—Natrix chrysarga, N. natrix.

Type locality.—Europe.

The genus *Leptophallus* has never been reported in America. Although type specimens are not available, the original description and drawing gave sufficient clue to the validity of placing it in the subfamily Brachycoeliinae.

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Limnology of the Middle Mississippi River and Adjacent Waters. Lakes on the Leveed Floodplain.[1]

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A survey of four lakes (Goose, Big, Sand, and Mud) on the floodplain of the Mississippi River near Quincy, in Adams County, Illinois, was conducted from August, 1949, to July, 1952, to study seasonal and annual variations in the plankton and the bottom fauna in relation to environmental factors.

All of the lakes included in this study occupied meander depressions formed by stream action on the floodplain. This is clearly shown in an aerial photo map of part of the South Quincy Drainage District (fig. 1). This map shows three of the lakes studied, as well as other bodies of water occupying parts of an old stream channel. Differences in natural and cultivated vegetation and in soil structure indicate former limits of the old channel, only a small part of which was occupied with water.

The lakes were very shallow, and the bottom, when exposed, presented a saucer-like form. They were of relatively uniform depth, and there were no deep parts. Any depression, such as that created by dredging, was soon obliterated by wave action which drifted bottom materials into the depression and filled it.

Finch and Trewartha (1936) have described the physiographic changes occurring as a result of stream action on a valley floor.

The lakes studied were rather unique in that the filling and obliterating processes were largely inoperative. All of the lakes lay in drainage districts which were completely separated from the river by artificial levees. Water which accumulated behind the levees was collected into drainage ditches and pumped over the levee at a central pumping station. The deposition of silt by floods was thus prevented, except at those infrequent intervals when the levee broke. In June, 1947, the levee of the South Quincy Drainage District was broken by high water, and a layer of silt several inches thick was deposited in all of the lakes of the district. Local fishermen claimed that this catastrophe had an important influence on the bottom of some

[1] This material was included in a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, University of Illinois. The author wishes to express his gratitude to Professor Max R. Matteson, under whose guidance the work was done, and to the Illinois State Academy of Science for a grant of funds. The aid of many other individuals is gratefully acknowledged, as follows: Dr. T. E. Larson, chemical problems; Dr. M. C. Old, Porifera; Dr. E. H. Ahlstrom, Rotifera; Dr. C. J. Goodnight, Oligochaeta; Dr. M. C. Meyer, Hirudinea; Dr. H. C. Yeatman, Copepoda; Dr. R. W. Kiser, Cladocera; Dr. W. L. Tressler, Ostracoda; Mrs. W. K. Gloyd, Odonata; Dr. H. B. Hungerford, Corixidae; Dr. S. S. Roback, Diptera; Dr. W. W. Wirth, Diptera; Dr. Frances Drouet, Blue-green Algae; Dr. Paul Silva, Algae.

of the lakes. Where sand bottoms formerly occurred, as at Sand Lake, for example, mud bottoms are now found.

Since the drainage area appeared to be generally limited in extent, and large parts of it were wooded, rain-washed sediments probably have had little influence on these lakes.

Aquatic vegetation was of little consequence in the economy of any of

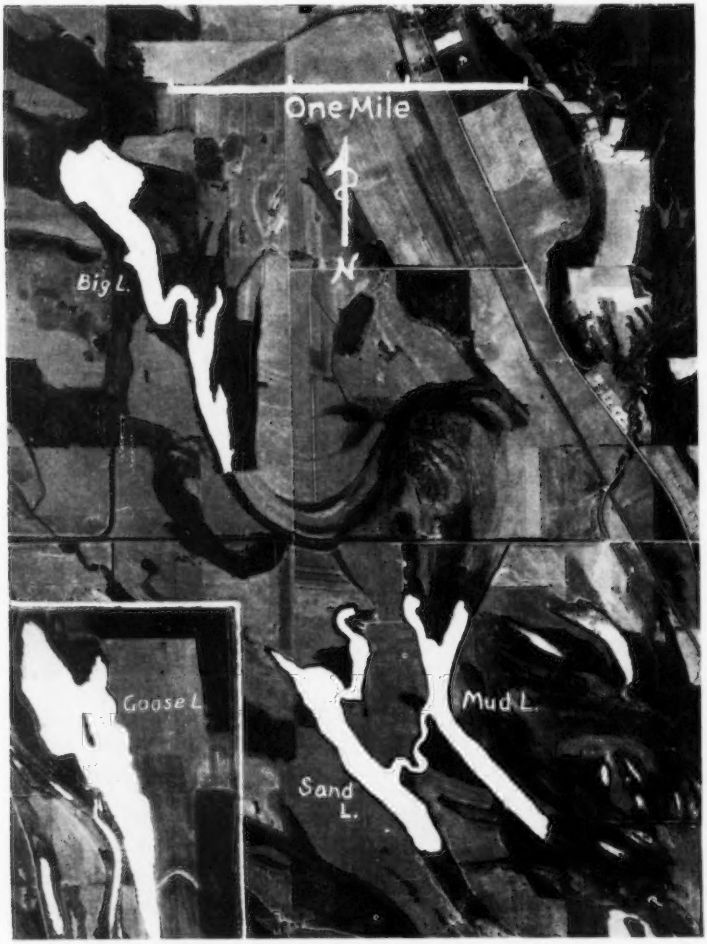


Fig. 1.—Aerial photo map showing location of oxbow lakes in relation to meander scars on floodplain of Mississippi River near Quincy, Illinois. Inset shows Goose Lake. The Mississippi River is on the left out of the picture, and the bluffs bordering the floodplain are to the right of the highway in the upper right hand.

these lakes; indeed, the lakes were notable for the lack of aquatic plants. Most of them were ringed with a narrow stand of willow (*Salix*) and cottonwood (*Populus*) trees. A few buttonbushes (*Cephalanthus*) stood in the water near shore. These trees and bushes contributed a considerable amount of debris to the bottom, but this debris was limited to a narrow margin around the edge of the lake. Goose Lake had a sparse growth of *Jussaeia* on the wet shore and at the water's edge. No floating or submerged vegetation was found in any of the lakes. High turbidity during the growing season, plus the activities of the bottom-feeding fishes made it impossible for plants of this kind to exist.

As a result of the reduction of the effect of the filling and obliterating processes, the existence of these lakes has been prolonged beyond the normal expectancy.

MORPHOMETRY

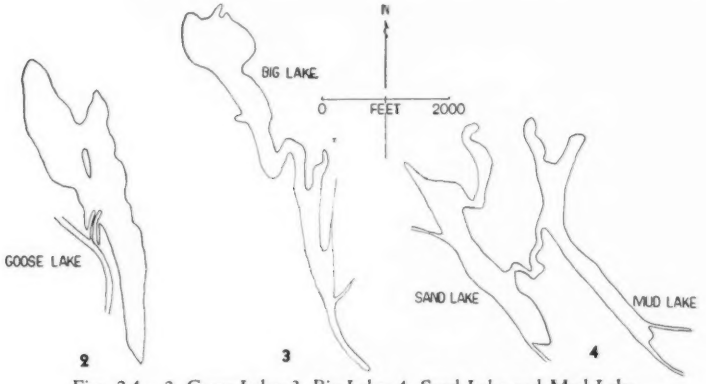
Morphometric data have been taken from maps of the Corps of Engineers, U. S. Army (1929-30), and from aerial photographic maps of the Production and Marketing Administration, U. S. Department of Agriculture (1950). These data were obtained as prescribed by Welch (1948). Area was determined by the weight method. Length of shore line was determined by the pin and thread method.

Goose Lake.—This lake (fig. 2), located in the Indian Grave Drainage District northwest of Quincy (in section 10, range 9W, town 1S), with a main axis in a NNW-SSE direction, has 1) an area of 63 acres, 2) a maximum length of 5,030 feet, 3) a similar maximum effective length (the single island probably interrupts the sweep of wind and wave action very little), 4) maximum width of 1,110 feet, 5) mean width of 550 feet, and 6) a shore line length of 12,620 feet. The index of shore development is 2.92. Measured depths ranged from a minimum of 24 inches to a maximum of 78 inches. This latter depth occurred in July and August, 1952, as a result of heavy rainfall in the area. A flash flood in the streams coming down from the uplands broke the levee and inundated a large part of the drainage district. The normal period of high water usually occurred in the winter or early spring months, and depths did not ordinarily exceed 48 inches.

The map (fig. 1) shows that only a small part of the shore line of Goose Lake was occupied by trees. Most of the east side and the north part of the west side was treeless. An island in the lake was covered by trees. The only extensive wooded area was on the southwest shore. At this place the banks were quite high. Since the prevailing winds were from the southwest in the summer, the combination of high banks with wooded shoreline tended to reduce wind action on parts of this lake at this season.

Most of the north part of the west side had a narrow sandy beach, or at least possessed a sandy bottom near shore. At one time the owner had attempted to deepen this part of the lake by dredging, but met with very limited success. The sandy bottom material was dredged out and piled upon shore. Wave action eroded the bank and washed all this material back into the lake in a few years.

Goose Lake was connected to the drainage system by a short ditch in the middle of the west side. The owner has tried to maintain a constant



Figs. 2-4.—2. Goose Lake; 3. Big Lake; 4. Sand Lake and Mud Lake.

water level in the lake by damming this ditch. Recently he strengthened this dam and installed an expensive drain tile and gate.

Lakes of the South Quincy Drainage District.—The other lakes lay in the South Quincy Drainage District, southwest of Quincy. In June, 1947, the levee enclosing this district was broken by high water in the Mississippi River. All of the lakes in the district were flooded to a depth of eight or ten feet above normal level. A layer of silt up to six to eight inches in depth was deposited over the district.

Big Lake.—This lake (fig. 3), owned by the Big Lake Hunting and Fishing Club (in sections 22, 26, and 27, range 9W, town 2S), with a main axis in a NNW-SSE direction, has 1) an area of 56 acres; 2) a maximum length of 6,760 feet; 3) a maximum effective length of 3,840 feet (because of the S-shaped bend at the middle of the lake); 4) a maximum width (north end) of 950 feet; 5) a mean width of 360 feet; and 6) a shore line 17,400 feet long. The index of shore development was 3.16. Measured depths ranged from 14 to 48 inches. Almost the entire shore line was ringed by at least a narrow margin of trees, and much of the adjacent lands were wooded. This lake was unique in that it was not directly connected with the general system of drainage ditches.

One of the important uses of all lakes in the Quincy area comes from duck hunting. Late summer droughts may cause some lakes to become nearly or completely dry. To forestall such a catastrophe, the Big Lake Club several years ago installed a pump in a deep well. Whenever water levels become low the pump is put into operation. The pump was operated for about three weeks after October 7, 1950.

Sand Lake.—This lake (fig. 4) (in section 35, range 9W, town 2S), with a main axis in a NW-SE direction, has 1) an area of 42 acres; 2) a maximum width of 580 feet; 3) a mean width of 490 feet; and 4) a shore line 11,840 feet long. The index of shore development was 2.49. Minimum and maximum depths were 16 and 60 inches respectively. The lake was

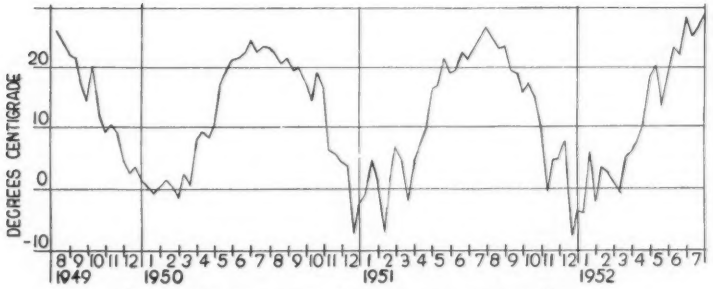


Fig. 5.—Air temperature, 10-day average, Quincy, Illinois.

formerly supposed to have had a sandy bottom. The flood of 1947 apparently deposited a heavy layer of silt, and only mud-covered bottom could be found.

Mud Lake.—This lake (fig. 4), east of Sand Lake (in sections 35 and 36, range 9W, towns 2S), has 1) an area of 38 acres; 2) a maximum length of 4,660 feet; 3) a maximum effective length of 3,180 feet; 4) a maximum width of 540 feet; 5) a mean width of 360 feet; and 6) a shore line 11,630 feet long. The index of shore development was 2.53. Minimum and maximum depths were 12 and 65 inches respectively.

Sand Lake and Mud Lake lay roughly parallel to one another. There were extensive woods at the north ends of both lakes, and between the south ends. Space rented on the lake shore for the construction of cottages was the only improvement attempted. A narrow, winding channel connected these two lakes. This channel appeared to be a natural feature, and usually the water in it was quite shallow.

SOILS OF THE BOTTOMLAND

Mozier et al. (1922) investigated the soil types associated with the lakes studied. *Drab clay* usually occurs at some distance from the river.

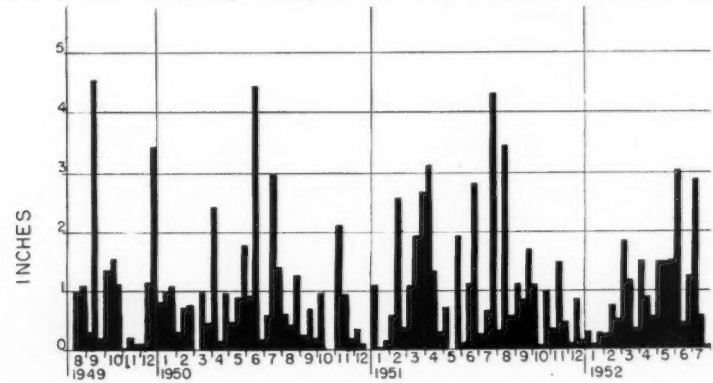


Fig. 6.—Precipitation, 10-day total, Quincy, Illinois.

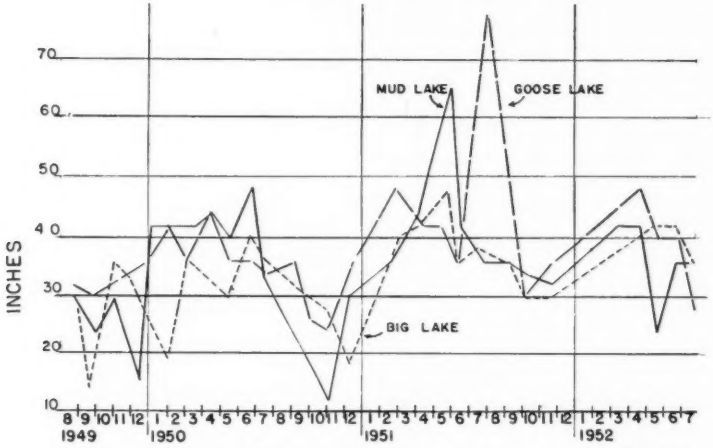


Fig. 7.—Depth of water at collecting stations, Mud Lake, Goose Lake, and Big Lake.

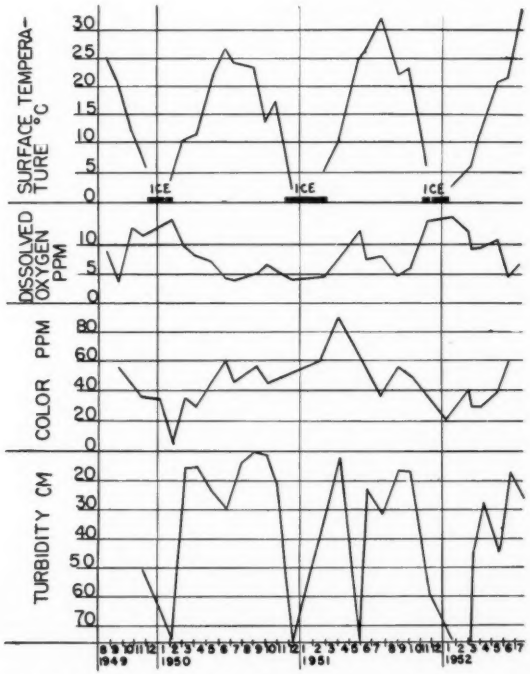


Fig. 8.—Big Lake. Turbidity, color, dissolved oxygen, and surface temperature.

It was formed where there was little current, so that it is composed of fine materials. This soil type was found at the north end of Big Lake, and surrounded the tip of the northwest arm of Goose Lake, and the south tip of Goose Lake. *Drab clay loam* is associated with drab clay, often intergrading with it. It contains more sand. All of Mud Lake and Sand Lake, the south half of Big Lake, all of the east side and the south half of the west side of Goose Lake lay in this soil type. *Brown sand loam* is generally distributed in the bottomland. It is sandy. The north half of the west side of Goose Lake was composed of this soil type. *Brown silt loam* was located between the two arms of Goose Lake. All of these soil types are reported as being deficient in lime.

PHYSICO-CHEMICAL CONDITIONS

Field observations and collections were made at approximately monthly intervals. Air temperature (fig. 5), and precipitation (fig. 6), were calculated for ten-day periods from data of the U. S. Weather Bureau (1949-1952). Ice on the lakes never attained a thickness exceeding six inches, and

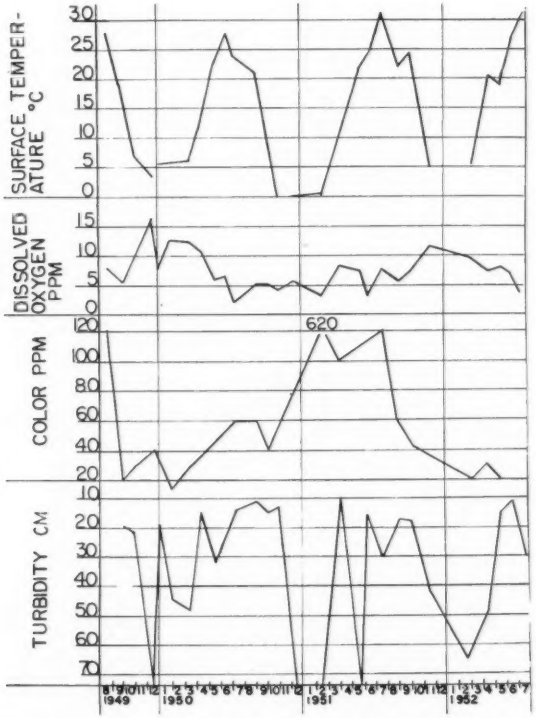


Fig. 9.—Mud Lake. Turbidity, color, dissolved oxygen, and surface temperature.

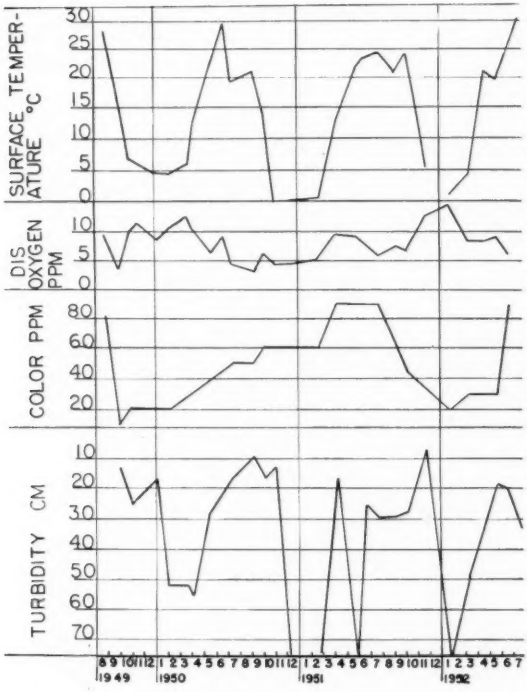


Fig. 10.—Sand Lake. Turbidity, color, dissolved oxygen, and surface temperature.

it occasionally melted during the winter. However, the ice cover lasted almost continuously for 90 to 100 days during the winter of 1951-1952. Water temperature (figs. 8 to 11), measured at the surface with a maximum-minimum thermometer, closely followed air temperature. Peaks in air temperature occurred in the summers of June, 1950, and July, 1951, and the water temperatures exhibited similar peaks.

Water samples were collected with a Kemmerer water bottle from the surface at the time and place of each bottom sample and dissolved oxygen was measured by the Rideal-Stewart modification of the Winkler method (figs. 8 to 11). Winter was frequently marked by the highest concentration of dissolved oxygen, but after the ice cover formed oxygen was somewhat reduced. The prolonged ice cover in 1950-1951 caused a modification of the typical winter condition. A cool-weather increase in dissolved oxygen began in some lakes, but the early formation of the ice cover prevented any great increase, and the winter was marked by low oxygen concentration in all lakes. Isolated peaks in dissolved oxygen occurred in all months of the year and there was no signficant correlation found between oxygen concentration and numbers of net phytoplankters. Dissolved oxygen frequently

fell to a low point during the summer months. These low concentrations probably were of importance in the survival of fishes, and deserve further study.

Color was measured with U. S. Geological Survey color standards. The amount of color present was highly variable. Low color in the winter months coincided with highest water levels (fig. 7), and the larger volume of water may have tended to dilute the color.

Turbidity measurements (figs. 8 to 11) were made with a Jackson turbidimeter. Ordinarily, the lakes were very turbid, and in the open water, the turbidimeter reading usually ranged between five and fifteen centimeters. Under ice, the water became relatively clear, and the turbidimeter reading often exceeded 75 centimeters.

Hydrogen ion concentration of water samples was measured in the field with Hellige pH color disks. Total alkalinity was determined by titration with .02N surfuric acid against methyl orange. Carbonate alkalinity was

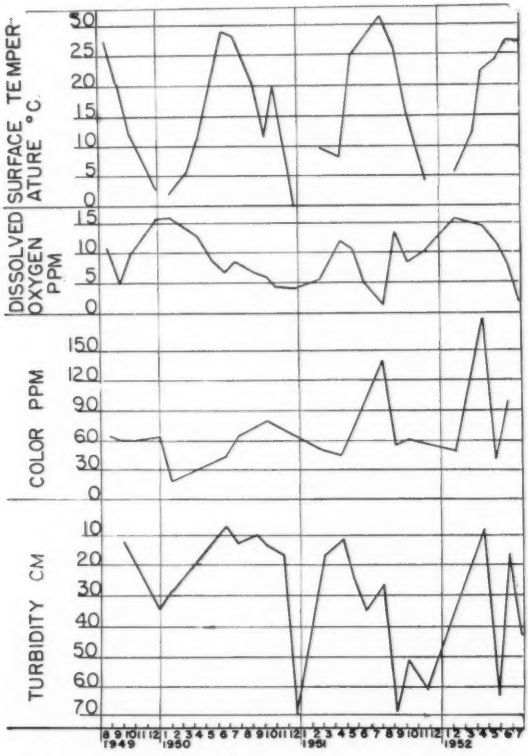


Fig. 11.—Goose Lake. Turbidity, color, dissolved oxygen, and surface temperature.

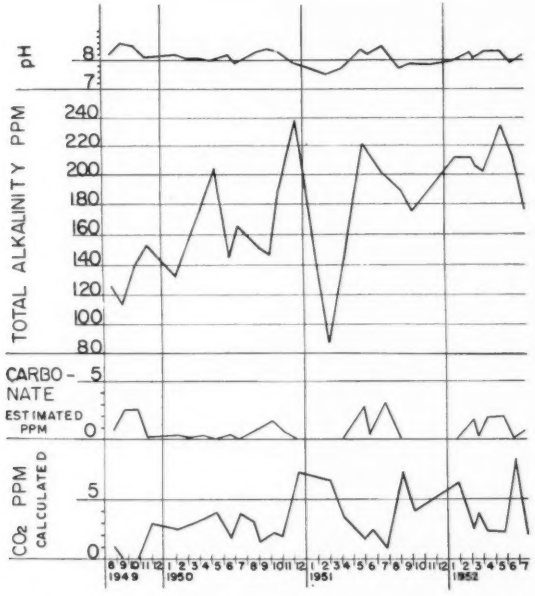


Fig. 12.—Big Lake. pH, total alkalinity, carbonates, and carbon dioxide.

estimated from total alkalinity and pH, using a nomogram published by the Permutit Company (1942). Free carbon dioxide was calculated according to the formula given by Larson and Buswell (1942) as follows:

$$\log CO_2 = \log \frac{.88}{K_1} + \log \text{alkalinity} - \text{pH} - .05,$$

where K, at $0°C = 2.61 \times 10^{-7}$
$10°C = 3.32 \times 10^{-7}$
$20°C = 4.05 \times 10^{-7}$
$25°C = 4.31 \times 10^{-7}$
$30°C = 4.52 \times 10^{-7}$
$40°C = 4.85 \times 10^{-7}$

The pH value generally had an inverse relation to the carbon dioxide concentration, particularly when alkalinity was low. This condition occurred in Goose Lake in December, 1950, and in August, 1951. The low alkalinity observed in January, 1950, and February, 1951, (figs. 12 to 15) occurred just after the ice had melted, and the surface water may have been somewhat diluted. In addition, much rain had fallen during the preceding ten days. A heavy rain on July 21, 1951, flooded Goose Lake and was followed

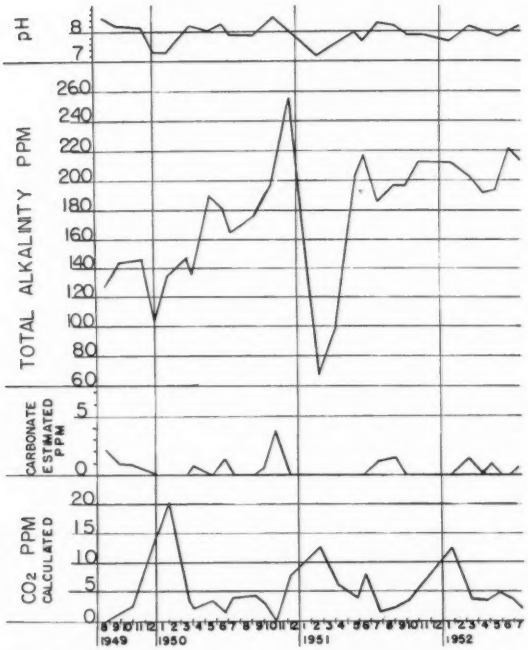


Fig. 13.—Mud Lake. pH, total alkalinity, carbonates, and carbon dioxide.

by low alkalinity in that lake. Most of these instances of lowered alkalinity probably may best be attributed to dilution of the water of the lakes by imported water low in carbonates. There was usually a low pH and a high concentration of carbon dioxide during the winter months, and a low carbon dioxide concentration during the summer. No significant correlation was found between free carbon dioxide and numbers of net phytoplankters.

Annotated list of organisms found in lakes

PROTOZOA

Frontonia sp., *Paramecium* sp., *Lacrymaria* sp., *Stentor* sp., *Arcella* sp., and *Difflugia oblonga* (?) were occasionally found in the plankton. *Vorticella* sp. was occasionally found attached to submerged objects. Other organisms which might be considered to be Protozoa are listed as algae.

PORIFERA

Meyenia crateriformis Potts (?) was occasionally found in the summer on the underside of submerged logs, especially between the loose bark and the trunk, where it formed flat, spreading masses up to two or three inches in diameter.

NEMATODA

One adult of *Limnomermis* sp. was taken from the bottom at Big Lake, November 28, 1949, and an adult of *Pseudomermis* sp. was taken at Mud Lake, June 16, 1950.

ROTIFERA

Anuraeopsis fissa (Gosse) was found in all lakes. It was common in Goose Lake, August, 1949, and Big Lake, October, 1951.

Asplanchna sp. occurred in all of these lakes in small numbers.

Brachionus angularis Gosse was a common and characteristic species, somewhat erratic in its seasonal distribution. Peaks were found at any season, but most commonly there seemed to be a winter or early spring minimum, with a maximum from April to August.

B. angularis chelonis Ahlstrom was common in Goose Lake in August, 1949. It is known from only a few other localities.

B. bidentata Anderson was found in Goose Lake, July 1950.

B. budapestinensis Daday usually appeared first in April or May, and disappeared by October.

B. calyciflorus Pallas was present in fairly large numbers in January and reached a maximum from March to June. It was usually absent from August or September until about the middle of the winter.

B. caudatus Barrois and Daday appeared first in late spring, and disappeared in early autumn.

B. havanaensis Rousselet occurred in all lakes in small numbers.

B. quadridentatus Pallas occurred in all lakes occasionally.

B. urceolaris Muller was found in Goose Lake, May, 1951; Sand Lake, March, 1950; and Big Lake, May, 1950, and May, 1951.

Cephalodella gibba (Ehrenberg) (?) was common in a collection from Big Lake, January, 1949.

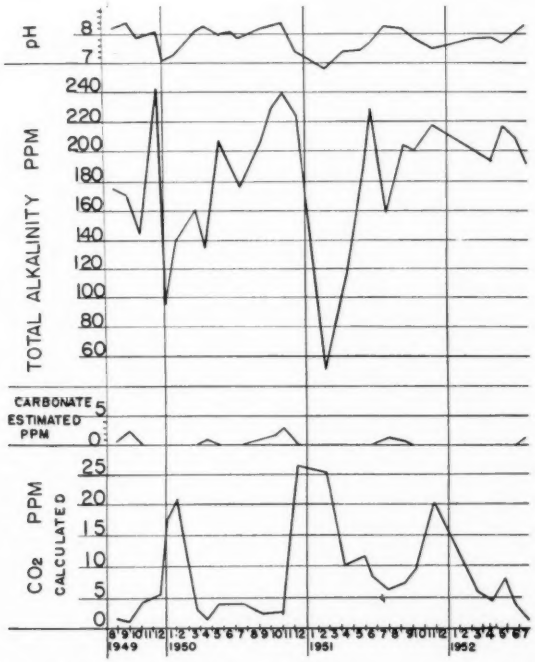


Fig. 14.—Sand Lake. pH, total alkalinity, carbonates, and carbon dioxide.

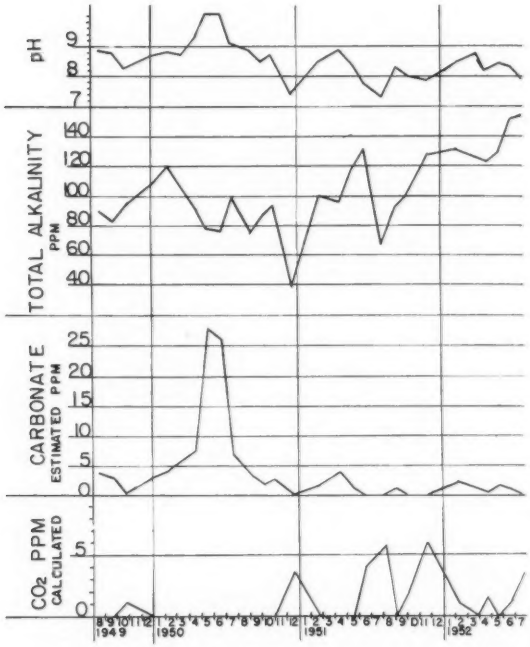


Fig. 15.—Goose Lake. pH, total alkalinity, carbonates, and carbon dioxide.

Filinia longiseta (Ehrenberg) first appeared during March or April, reached a maximum in midsummer, and disappeared after September.

F. brachiata (Rousselet) (?) was found in Big Lake, December, 1950, and October, 1951.

Kellicottia bostoniensis (Rousselet) was rather common in Big Lake, April, 1951. According to Dr. Ahlstrom this species is not as common in various parts of the country as *K. longispina*.

Keratella cochlearis (Gosse) and *K. cochlearis tecta* Lauterborn were the most common members of this genus, which could be found at nearly all seasons, with peaks in abundance occurring in almost every month. Minimum populations frequently occurred in midsummer. *K. gracilenta* Ahlstrom was common in Goose Lake, July, 1950. *K. valga* Ehrenberg was rather common in a small pond near Big Lake, April, 1951.

Lecane luna (Muller) was found once in a small pond near Big Lake, August, 1949.

Monostyla bulla Gosse, and *Monostyla hamata* Stokes were found very rarely.

Notholca acuminata (Ehrenberg) was occasionally found in small numbers.

Pedalia sp. occurred from May to September.

Platyias patulus (Muller) was found in the small pond near Big Lake, October, 1949, and July, 1950.

Polyarthra trigla Ehrenberg was year-around in occurrence, with the minimum occurring in the winter.

Synchaeta sp. occurred in small numbers, about as frequently in the cold months as in the warm months.

Tetramastix opoliensis brevispina Ahlstrom was rather common in a small pond near Big Lake, August, 1949, and July, 1950. It has not been reported from this country.

This variety was described by Ahlstrom from Mexico, and reported by him from Brazil. Dr. Ahlstrom also has seen material from Argentina, India, and Florida.

Trichocerca multicrinis (Kellicott) and *Trichocerca* (*Diurella*) *tenuior* (Gosse) were each found once in the small pond near Big Lake.

T. pusilla (Jennings) and *T.* (*D.*) *stylata* (Eyferth) were common, reaching their greatest abundance in late summer.

ANNELIDA

OLIGOCHAETA

Sparganophilus sp. was found in the sandy beach and under logs and other debris at the water's edge at Goose Lake. It was found in large groups in shallow water in small dredged pools at the northwest end of Goose Lake.

Peloscolex multisetosus (Smith) was an important constituent of the bottom population in all lakes. The maximum tubificid population usually occurred in the winter or spring months, and the minimum often occurred some time in the summer (fig. 16). Cocoons were most frequent from March to May, but were also common in the period from October until December or January. At those times when the tubificid population was at a

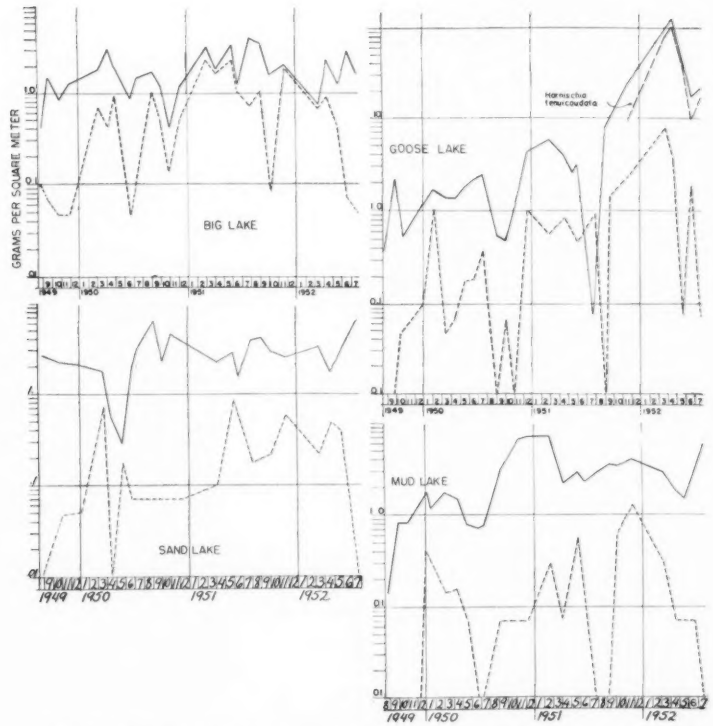


Fig. 16.—Weights of bottom organisms, gms/m^2. Dotted line = tubificids. Solid line = total organisms, except as indicated. Ordinates of graphs show grams/meter^2 on a logarithmic scale.

low point, the collections were frequently composed of numerous small pieces of worms which were somewhat decayed. These observations suggest a periodic dying-off of the whole population. However, cycles of abundance and scarcity were so irregular that it was difficult to correlate these phenomena with reproductive cycles or environmental factors.

HIRUDINEA

Glossiphonia fusca Castle was collected at Goose Lake from debris at the water's edge, June 24, 1952.

Placobdella montifera Moore was collected from mussels at Sand Lake, October 4, 1950, and from a boat at Goose Lake, August, 1951, and from Mud Lake, October, 1951.

Helobdella stagnalis (Linnaeus) was collected in a bottom sample, Goose Lake, March, 1952.

Erpobdella punctata (Leidy) was collected from debris at the water's edge at Goose Lake, June, 1952, and July, 1952.

ARTHROPODA

CRUSTACEA

COPEPODA

Cyclops vernalis Fischer was one of the more common copepods. Adults were found at all seasons.

C. bicuspidatus Claus occurred rarely. Adults were collected in February.

Mesocyclops edax Forbes was found in Big Lake, and in Mud Lake from late June until January or February.

Eucyclops agilis (Koch) was found once in Sand Lake in November.

Trophocyclops prasinus Fischer was found once in Sand Lake in November.

Canthocamptus staphylinoides Pearse was found in Big Lake in February.

Diaptomus siciloides Lilljeborg was a common and abundant species, found at all seasons.

Ergasilus chatauquaensis Fellows was found in Goose Lake and Sand Lake in August, 1949, and in Sand Lake, July, 1950. This "parasitic" copepod has been recorded only from Lake Champlain, N. Y., and Lake Mendota, Wisconsin.

CLADOCERA

Daphnia pulex parapulex breviceps (Birge) was the most common and abundant of the Cladocera, occurring from April or May until October.

Ilyocryptus sordidus (Lieven) occurred rarely.

Diaphanosoma brachyurum (Lieven) was rather common during the summer.

Moina brachiata (Jurine) (?) occurred from April until August.

Bosmina longirostris var. *cornuta* (O. F. M.) was common in the summer.

Ceriodaphnia pulchella Sars was occasional in the summer.

OSTRACODA

Candona crogmaniana Turner was found occasionally in collections from the open water, most commonly in the winter or spring.

AMPHIPODA

Hyalella azteci Saussure was occasionally collected near shore.

DECAPODA

Cambarus immunis Hagen adults were collected from Goose Lake and young were collected from Sand Lake, June, 1952.

Palaemonetes exilipes Stimpson was taken with the dipnet around the edges of the lakes, and was found with eggs at Big Lake, May, 1950.

INSECTA

EPHEMERIDA

Caenis sp. was taken at Sand Lake, May, 1952.

ODONATA

Ischnura verticalis (Say) nymph was taken at Goose Lake, May, 1950, and at Sand Lake, May, 1952.

I. posita (Hagen) nymph was taken at Goose Lake, May, 1950.

Enallagma signatum (Hagen) nymph was taken at Sand Lake, May, 1952.

Gomphus (*Arigomphus*) *submedianus* Williamson nymph was taken at Big Lake, January, 1948.

Argia violacea (Hagen) nymph was taken at Sand Lake, May, 1952.

Nasieschna pentacantha (Ramb.) nymph was taken at Big Lake, August, 1950.

HEMIPTERA

Trichocorixa verticalis (Fieber) adults were collected at Big Lake, January, 1948, and March, 1950.

Sigara alternata (Say) adults were collected at Big Lake, January, 1948, and March, 1950.

DIPTERA

CULICIDAE

Chaoborus (*Corethra*) *punctipennis* (Say) larvae formed an important part of the bottom fauna of all lakes. Pupation and emergence of the adults usually occurred in late summer. Numbers decreased through the winter (fig. 18). An anomalous late spring increase occurred. Study of this and other insect larvae is being continued, and will form the subject of a later paper.

Psorophora ciliata (Fabricius) adults were rather common at Goose Lage, August, 1951.

EPHYDRIDAE

Parydra sp. adults were collected at Goose Lake, June 7, 1950.

TENDIPEDIDAE (CHIRONOMIDAE)

Pelopia (*Tanypus*) *stellata* (Coquillett) larvae were occasionally found.

P. sp. (*Tanypus* species B of Malloch, 1915) larvae occurred in the open water from late May until September. During the remainder of the year, they were completely absent from the open water and appeared to be located in the shallow water near shore. This species may have a two-year life cycle.

Procladius culiciformis (L.) and *Procladius* nr. *adumbratus* Johannsen larvae cannot be satisfactorily separated. The graph (fig. 17) contains both species. The presence of two peaks in the summer probably indicates different times of emergence of these two species, but this question cannot be satisfactorily answered at the present time.

Clinotanypus sp. larvae were collected at Mud Lake, June, 1951.

Coelotanypus concinnus (Coquillett) larvae occurred in small numbers in all of the lakes. The available data seem to indicate that this species has a two-year life cycle.

Glyptotendipes lobiferus (Say) adults were collected at all of the lakes, and larvae were occasionally found in the bottom collections. Adults taken at Goose Lake, June, 1950, were gynandromorphs.

Cryptochironomus digitatus (Malloch) larvae were occasionally collected.

C. pararostris Harnisch larvae were collected at Big Lake, December, 1948.

Harnischia tenuicaudata (Malloch) larvae were rarely found in any of the lakes until after the summer flood at Goose Lake. A discussion of this species is given in the section on the effects of flooding.

Tendipes (*Limnochironomus*) *nervosus* (Staeger) adults were taken at Goose Lake, June, 1950, and at Sand Lake, June, 1952.

T. dorsalis (Meigen) larvae were collected at Mud Lake, April, 1952.

T. crassicaudata (Malloch) larvae were collected at a small pond near Big Lake, May, 1952.

HELEIDAE

Atrichopogon sp. adults were collected at Goose Lake, June, 1950.

Palpomyia sp. larvae were occasionally found in small numbers in all lakes.

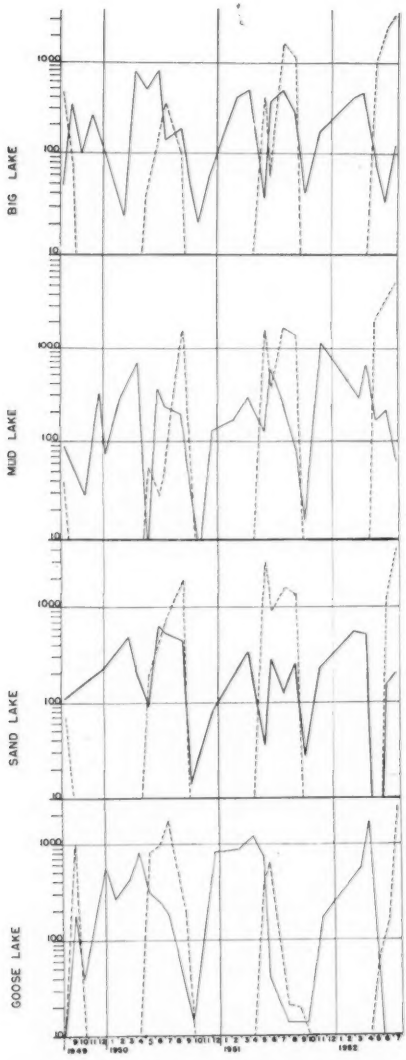


Fig. 17.—Numbers of bottom organisms/m^2. Dotted lines = *Pelopia* (*Tanypus*) sp. Solid lines = *Procladius* spp. Ordinates of the graphs show numbers/m^2 on a logarithmic scale.

MOLLUSCA

PELECYPODA

Anodonta corpulenta Cooper and *A. grandis footiana* Lea were collected in a channel between Mud Lake and Sand Lake at the time of low water in October, 1950.

GASTROPODA

Physella sayii crassa Walker was frequently found on the submerged debris at the edge of all the lakes. It was infected with a cercarieaum in the winter of 1951-1952 at Goose Lake. This species and *Helisoma antrosa percarinata* (Walker) and *H. trivolvis* (Say) were associated in small dredged pools connected to the northwest end of Goose Lake.

Ferrissia spp. were collected at Sand Lake, April, May, and September, 1950.

During the summer of 1951, material to strengthen the dam was dredged from the bottom of Goose Lake. From this material, the dead shells of 11 or 12 species of mussels and snails were obtained as follows: *Anodonta grandis footiana* Lea, *Megalonaias gigantea* (Barnes), *Quadrula quadrula* Rafinesque, *Amblema peruviana* (Lamarck), *Obliquaria reflexa* Rafinesque, *Pleurobema pyramidatum* (Lea), *Sphaerium* sp., *Campeloma rufum* and/or *C. decisum, Lioplax subcarinata* (Say), *Pleurocera acuta* Rafinesque (?), and *Viviparus contectoides* W. G. Binney (?).

These molluscs are inhabitants of running water, and are typically Mississippi River forms. Of the species listed, only *Anodonta grandis footiana* has been found alive in these lakes. Most of the specimens collected were generally smaller than the typical form, and were either young or dwarfed shells.

CHORDATA

A discussion of the fish populations of these lakes forms the subject of another paper which is in the process of preparation.

CYANOPHYTA

Aphanizomenon flos-aquae Born and Flah. was occasionally very abundant in Goose Lake, where it appeared in especially large numbers in 1950. Other blue-green algae found in the plankton were: *Anacystis montana* (Lightf.) Drouet and Daily, *A. incerta* (Lemm.) Drouet and Daily, *Anabaena flos-aquae* Born. and Flah., *A. circinalis* Born. and Flah., *Oscillatoria agardhii* Gomont, *Pleurocapsa minor* (?), *Cylindrospermum* sp., *Microcystis aeruginosa* Kuetz., *Merismopedia tenuissima* Lemmermann (?), *Coelosphaerium kuetzingianum* Naegeli.

CHLOROPHYTA

The following species of green algae were identified in the plankton: *Carteria* sp., *Gonium* sp., *Pandorina morum* (Muell.) Bory, *Volvulina* (?) sp., *Eudorina elegans* Ehrenberg, *Platydorina caudata* Kofoid, *Volvox aureus* Ehrens., *Uronema* (?) sp., *Ulothrix* (?) sp., *Micractinium pusillum* Fresenius, *Actidesmium* sp., *Pediastrum simplex* var. *duodenarium* (Bail.) Raben., *P. biradiatum* Meyen, *Coelastrum microporum* Naegeli, *Closteriopsis* sp., *Dictyosphaerium ehrenbergianum* Naegeli, *Oocystis* sp., *Selenastrum westii* G. M. Smith, *Tetraedron trigonum* (Naegeli), *T.* sp., *Echinosphaerella limnetica* G. M. Smith (?), *Treubaria* sp., *Trochiscia reticularis* (Rainsch) (?), *Actinastrum hantzschii* var. *fluviatile* Schroeder, *Scenedesmus dimorphus* (Turpin) (?) Kuetzing, *S. quadricauda* (Turpin) de Brebisson, *Staurastrum* prox. *paradoxum, S. johnsonii* W. and G. S. West.

EUGLENOPHYTA

The following euglenophytes were found in the plankton: *Euglena antefossa* Johnson, *E. acutissima* Lemmermann, *E. proxima* Dangeard, *E. spirogyra* Ehrenberg, *E. acus* Ehrenberg, *Phacus curvicauda* (?), *P. longicauda* (Ehrenberg) Dujardin, *P. tortus* (Lemm.) Skvortzov, *P. helicoides* Pochmann, *Trachelomonas girardiana* (Playf.) Deflandre, *T.* spp.

CHRYSOPHYTA

Tribonema sp., *Synura uvella* Ehrenberg, *Dinobryon* sp. and *Botryococcus* sp. were found in the plankton.

Synedra acus (?) was rather common in the plankton, and *Pleurosigma* sp. was also present occasionally. *Stephanodiscus* sp. was found in Goose Lake at the time of the

flood, August, 1951. It was not seen at any other time in these lakes. It is commonly found in the river plankton.

PYRROPHYTA

Glenodinium gymnodinium (?), and *Ceratium hirundinella* (Muell.) Schrank. were common plankters.

BOTTOM FAUNA

Bottom samples were collected with a six-inch Ekman dredge. The dredged material was washed through a 40-mesh screen, and the residue was immediately preserved in formalin. In the laboratory all organisms were removed from the whole sample, counted, and weighed, except for the tubificids, which were weighed, but not counted. Organisms to be weighed were first rolled dry on paper. The dredge hauls were made at established stations located about equidistant from the two nearest shores. The boat was moved after each dredge haul, so that collections from each station were distributed

TABLE 1.—Analysis of organisms found in bottom samples along transects from shore. Numbers and grams/m^2.

	Goose Lake, May 24, 1952					
Stations	1	2	3	4	5	6
Distance from shore (meters)	8	12	16	20	24	center
Species						
Tendipes (*Chironomus*) spp.	176	0	48	96	64	14
Harnischia tenuicaudata	32	294	288	320	400	574
Proclaudius spp.	960	168	1680	1104	1232	455
Pelopia (*Tanypus*) sp.	64	70	816	1024	944	630
Chaoborus (*Corethra*) *punctipennis* larvae	0	987	720	1280	1892	2646
Chaoborus pupae	0	203	96	304	368	581
Heleidae (Ceratopogononidae)	64	175	352	288	32	364
Coelotanypus concinnus	16	14	96	16	0	28
Total	1312	1911	3696	4432	4932	5292
Tubificid weights (wet)	1.536	0.0	8.448	9.472	4.765	7.308
Total weights (wet)	4.128	8.543	33.120	40.896	47.552	59.038

	Sand Lake, May 22, 1952						
Stations	1	2	3	4	5	6	7
Distance from shore (meters)	12	18	24	30	36	42	48
Species							
Tendipes (*Chironomus*) sp.	40	20	40	100	10	100	14
Procladius spp.	150	120	60	130	70	170	154
Pelopia (*Tanypus*) sp.	1090	1450	650	1160	730	1280	1330
Chaoborus (*Corethra*) *punctipennis* larvae	70	160	240	160	260	230	350
Chaoborus pupae	10	40	20	20	80	20	42
Heleidae (Ceratopogonidae)	50	20	0	70	0	10	21
Total	1410	1710	1010	1640	1150	1810	1911

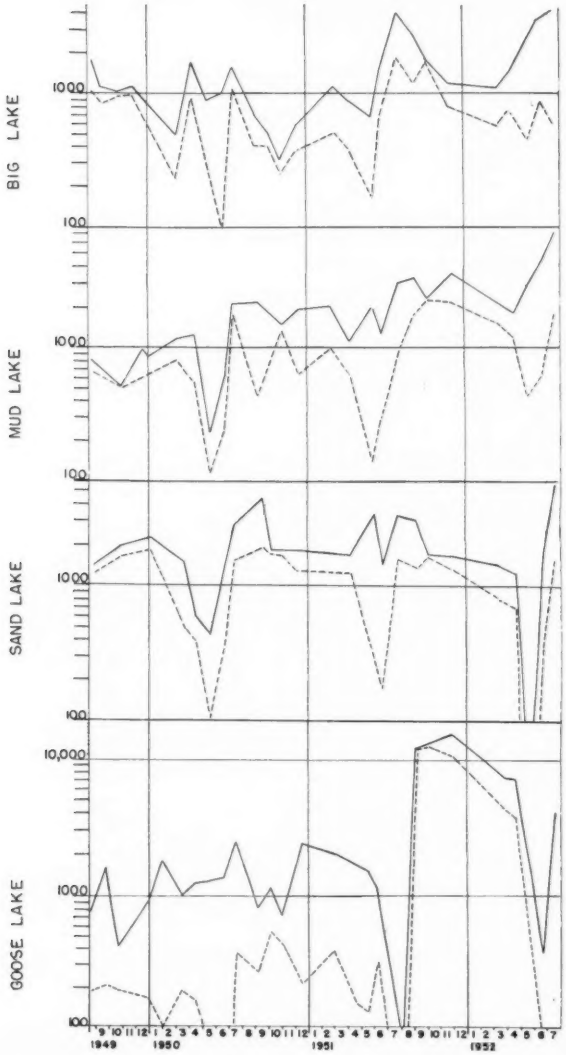


Fig. 18.—Numbers of bottom organisms/m^2. Dotted lines = *Chaoborus* (*Corethra*) *punctipennis*. Solid lines = total larvae. Ordinates of the graphs show numbers/m^2 on a logarithmic scale.

over a relatively wide area. From two to nine dredge-hauls were made at each collection and combined into a single sample.

Little effort was made to collect near the shore because the large amounts of heavy debris composed of large limbs, twigs, and leaves from the trees on shore could not be handled satisfactorily with the available quipment. However, a few transects were made which included this area. Table 1 shows the numbers of each species and the total number of insect larvae at Goose Lake and at Sand Lake, and the weights of tubificids and the total weights of all organisms at Goose Lake. At Goose Lake there was a progressive increase in both total numbers of insect larvae and total weights of all organisms from the stations nearest shore toward the center of the lake. At Sand Lake there was a general increase from shore toward the center, but the distribution at intermediate stations was somewhat erratic. *Chaoborus punctipennis* showed a decided preference for the more central locations. This fact is of interest in connection with the observations of Eggleton (1931), and Juday (1921), who reported that this species was more abundant in deeper water. *Harnischia tenuicaudata* appeared to prefer the more central location, also. Other species exhibited a somewhat irregular distribution.

EFFECT OF CATASTROPHIC EVENTS ON THE BOTTOM FAUNA

Winterkill.—During the winter of 1950-1951, ice covered the lakes for about 90 days. Dissolved oxygen concentration fell very low during this

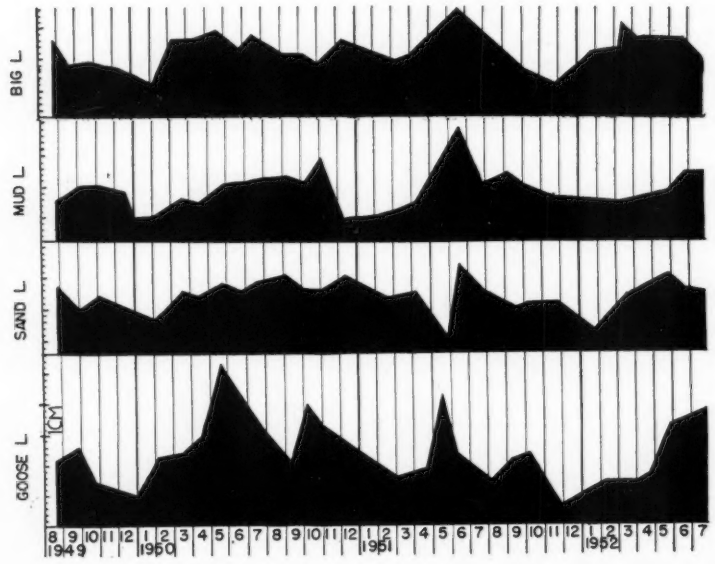


Fig. 19.—Total zooplankton. Numbers/meter^3 are plotted according to the method of Lohman. The scale on the ordinates is in millimeters.

period, and mortality of fishes was heavy. Collections of plankton and bottom fauna were made at Goose Lake a few days after the ice had melted. Dead larvae of *Chaoborus punctipennis* were observed floating at the surface. It is probable that these larvae had died as a result of the conditions imposed by the ice cover. However, the data (figs. 16, 17, and 18) do not indicate any great or unusual reduction in numbers of this species, nor indeed, of any other component of the bottom population. Environmental conditions during this winter probably were about as severe as they ever can be in this locality, yet the bottom fanua did not suffer ony great harm.

Flood.—During the night of July 22, 1951, 4.5 inches of rain fell at Quincy. North of Quincy, the streams carrying water down from the uplands flooded Goose Lake and the adjoining farmlands. When Goose Lake was visited August 2, a great number of buffalo-fish were found dead and in an advanced state of decomposition. The dissolved oxygen concentration was only 1.4 ppm (fig. 11). This reduction of dissolved oxygen may have resulted from bacterial decomposition of organic materials brought into the lake by the flood. The metabolic nature of the situation is further indicated by the fact that the free carbon dioxide was high at the same time (fig. 15), and net phytoplankton was low (fig. 20).

The available evidence indicates that this flood and the accompanying reduced dissolved oxygen had an adverse effect on some of the bottom organisms. The total number of insect larvae was reduced to a point considerably lower than that observed at any other time at Goose Lake (fig. 18). The numbers of *Procladius* spp. larvae declined at the time of the flood and did not increase until October (fig. 17). Ordinarily, the late summer decrease of these larvae did not come until September or October. *Coelotanypus concinnus* and *Pelopia* sp. larvae decreased markedly in numbers (fig. 17). The tubificid population was not affected, but remained at a high point until September. It was not uncommon for tubificid populations to decrease to a low point in September. From these data it appears that very low dissolved oxygen at the season of high temperature is inimical to the insect fauna of the lake bottom.

FISH PREDATION AS A CONTROLLING FACTOR

There was an unusually high production of bottom organisms at Goose Lake during the winter and spring following the flood of July, 1951. The total numbers of insect larvae rose from a minimum of 77 per sq. m. at the time of the flood to a maximum of more than 20,600 per sq. m. in late November. The bottom population in September was composed almost entirely of young *Chaoborus* larvae. After the end of October, the *Chaoborus* population declined throughout the winter until pupation began in May. About the middle of November, nearly 10,000 larvae of *Harnischia tenuicaudata* per sq. m. were present. The numbers of *Harnischia* then declined until July, when there were 140 per sq. m., and the average weights rose from 0.0011 g to 0.123 g. Throughout the period of decline in numbers, dead larvae of *Harnischia* were found in the collections, indicating a continuing mortality of rather large proportions. Growth of these larvae resulted in a peak in weight of 125.7 g per sq. m. in late April. The tubificid

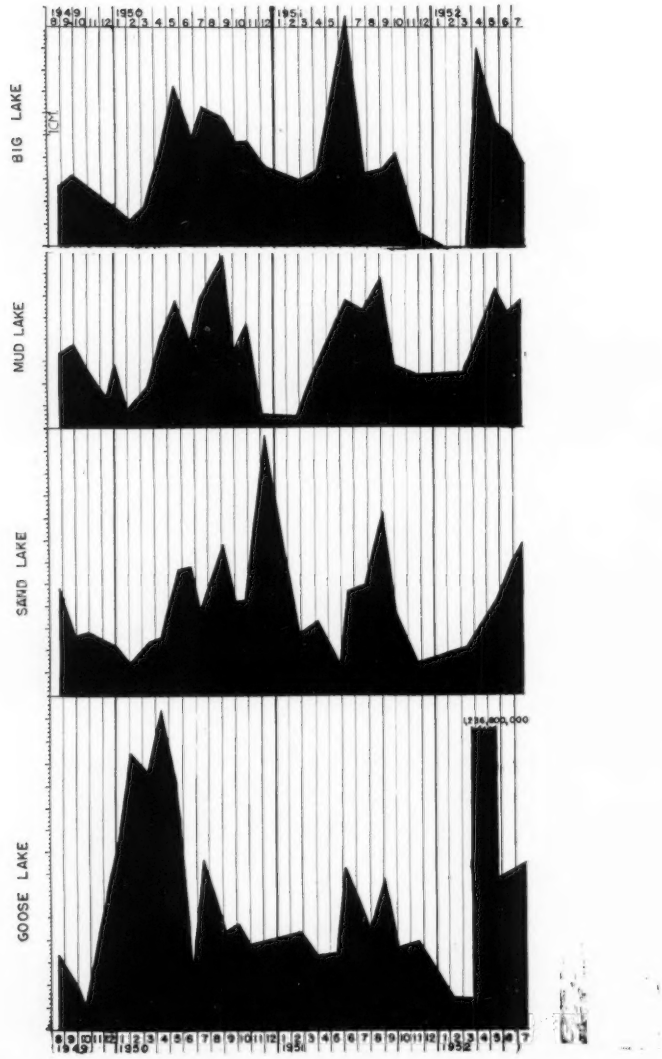


Fig. 20.—Total net phytoplankton. Numbers/m^3. See note on figure 19.

population increased until late March, when a weight of 7.7 g per sq. m. was attained. This was almost eight times the greatest weight of tubificids previously observed in this lake.

Commercial fishing and the winterkill during the winter of 1950-1951, and the high mortality following the flood of July, 1951, undoubtedly reduced the fish population to a low level in Goose Lake. Many of the fish which had formerly been present are usually considered to be bottom feeders. The elimination of these bottom feeders relieved the predation pressure on the bottom organisms, so that reproduction success and survival of the young was greatly increased. This would seem to be the most logical explanation for the great increase in the numbers of bottom organisms in the winter and spring of 1951-1952. Another possible explanation for the increase in bottom fauna is that the decomposition of the dead bodies of the fish enriched the water. If the bottom fauna could have derived any benefit from this source, it would seem that the plankton would also benefit and would increase. However, both zooplankton and net phytoplankton were low during the winter and spring of 1951-1952, in fact much lower than in previous years (figs. 19 and 20).

PLANKTON

Plankton samples were obtained by dipping up water from just below the surface and pouring it through a plankton net of No. 20 mesh. The plankton in nineteen liters of lake water was concentrated into about 100 ml

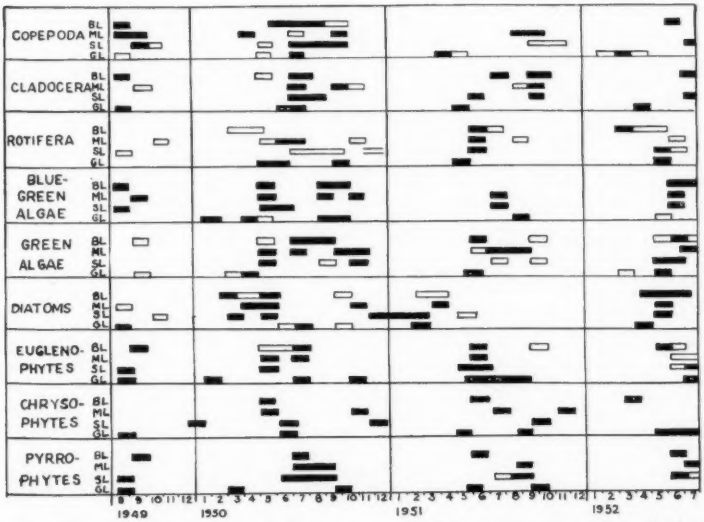


Fig. 21.—Seasonal pulses in plankton groups. Black bars represent numbers of plankters twice the annual mean. White bars represent numbers one and one-half times the annual mean. Each bar arbitrarily extends half-way in each direction to the next date. Names of lakes are abbreviated as follows: BL = Big Lake, ML = Mud Lake, SL = Sand Lake, GL = Goose Lake.

and preserved in formalin. Because of the presence of large amounts of suspended materials throughout most of the year, collections of nannoplankton made by settling and decantation were unusable. Numbers of net plankters per cubic meter were calculated from counts in the Sedgwick-Rafter cell.

A plankton pulse is arbitrarily defined by Pennak (1946) as a number of organisms twice the annual mean. This condition is shown for each plankton group in each lake of the present study by solid bars in fig. 21. The open bars represent numbers which are one and one-half times the mean. The annual mean was calculated from August to July of each year of the study. The nine major plankton groups shown are those which occurred in sufficient frequency and abundance to warrant analysis. Protozoa are not represented, chiefly because many organisms which might be considered to be Protozoa are included with the phytoplankton.

There is a great deal of variation between lakes in each year for each group. Net plankton populations appeared to have been concentrated in the summer months of 1950 much less than in other years. This is indicated by the more frequent occurrence and longer duration of maxima throughout much of the whole year.

The copepods were present in greatest abundance during the summer or fall. Copepod pulses, or increases in population, occurred three times in April, four times in May, seven times in the fall from September to November, and in three cases, two or more times in the summer. The Cladocera exhibited the same general pattern of distribution as the Copepoda, except that there was somewhat less evidence of a spring maximum. The rotifers presented an irregular pattern of seasonal distribution. During 1950, increases occurred from January to December, while during 1951, and possibly 1952, the increases were concentrated in the summer months. The blue-green algae showed a distributional pattern similar to that of the rotifers. Increases were found at all seasons except midwinter in 1950, but the maxima appeared in summer in 1949, 1950, and 1952. In 1950 pulses in the green algae were present irregularly from spring to autumn and in 1951 late spring and autumn maxima were fairly well marked. 1952 showed promise of a distributional pattern similar to that of 1951. Desmids never represented an important part of the total population. Diatom pulses were very irregular and populations were generally low except on a few occasions of exceptionally large increases. A winter maximum appeared on one occasion. In 1950, pulses were found at all seasons, and in 1951 were limited to the spring. The euglenophyte pulses were definitely limited to the summer months. The chrysophytes exhibited an irregular distributional pattern. Populations of these forms were generally erratic in numbers and distribution. The pyrrophytes, like the euglenophytes, were generally limited to the summer months.

Somewhat more regular patterns appeared when total net zooplankton and net phytoplankton populations were considered. The graph of total net zooplankton (fig. 19) includes Copepoda, Cladocera, and Rotifera. Populations of zooplankters were considerably lower in numbers than those of phytoplankters. The seasonal distribution of zooplankton appeared to be somewhat erratic. Winter populations were frequently low, but at times, were relatively high. The highest points reached by zooplankton occurred from February to November. The most common feature of net phytoplankton

distribution (fig. 20) was the occurrence of large populations during the summer. There was frequently a peak in April or May, and another in July or August or early September. Winter populations were generally very low. An unusual spring peak composed largely of *Aphanizomenon* filaments occurred at Goose Lake in 1950.

DISCUSSION

The work by Eddy (1934) and Gersbacher (1937) on aquatic communities in Illinois has shown that community development or biotic succession is a guide to the classification of freshwater communities, at least of those in the stream series. From his studies on plankton, Eddy found that stream communities belong to an aquatic association, of which a stable river community is the climax. He found four general types of plankton societies, of which two appear to be related to the stream series: rivers and related waters exhibiting some degree of stability, and temporary ponds. Such societies are characterized by predominent plankton forms which are the same in perennial ponds and shallow lakes as those in mature rivers. Waters which are abandoned parts of streams contain communities which are "retrograding" from the aquatic climax. They are at some stage in succession towards a terrestrial climax, and are part of the terrestrial association. As succession progresses, these waters will become temporary ponds, and the plankton society will be composed of a new set of predominants. The sequence of successional events is 1) stable stream climax, 2) abandoned stream waters, 3) temporary ponds, and 4) terrestrial series. The plankton predominants of the stable stream climax and the abandoned stream waters are the same, and include several species of *Brachionus, Filinia longiseta, Synchaeta* spp., *Cyclops vernalis* (*viridis*), *Diaphanosoma brachyurum, Polyarthra,* and *Keratella.* The plankton predominants of temporary ponds are *Simocephalus* spp., *Camptocercus, Eucyclops agilis* (*Cyclops serrulatus*), *Cyclops bicuspidatus, Polyarthra, Keratella,* and *Cyclops vernalis.*

Gersbacher (1937), who studied the bottom fauna, suggested the existence of a single major stream community and its developmental stages and variations. He stated that a climax bottom community exists where physiographic conditions permit the formation of mud-bottomed pools. The physiographic climax community is essentially without rooted vegetation. Insects and molluscs are predominant, and fishes are the most important dominants.

The work of Cahn (1929) has shown the effect of the activities of the European carp on the aquatic habitat. This fish, by its feeding activities, increases greatly the turbidity and roots out aquatic plants. The carp draws bottom material into its mouth and then forcibly expels it, causing the fine mud of the bottom to be swept away. This is probably the most important means by which the carp increases turbidity. Plants not directly killed by the carp are eliminated by the suspended silt which shuts out light. Many species of fishes are eliminated, apparently by the destruction of nests.

Clements and Shelford (1939) state that separation of an oxbow pond from the river channel immediately starts the pond in a land sere, characterized by increases in vegetation, and extinction of the bottom community. This separation and the stoppage of current constitute a fundamental change

in aquatic climate, and the fishes are unable to retard the process. In their view, the development of seral land communities should speedily occur and fill up and destroy the shallow lakes of the present study. However, it appears that removal of these lakes from stream conditions has not resulted in very great progress toward a terrestrial sere, but that the dominant fishes, with the aid of other factors, have maintained conditions of a quasi climax nature past the normal term. Many of the characteristic river fishes are important elements in the fauna of the bottomland lakes and have continued to exercise a considerable degree of control over the habitat. Shelford suggests that native fishes found as permanent residents in river pools and bottomland lakes must also have the same effect as the carp, since their feeding activities are similar to those of the carp. The absence of aquatic vegetation from these lakes is an important feature. Garman (1890) in his study of some of these lakes in 1888 found a notable lack of rooted and submerged or floating aquatic plants. Garman's work was done only a few years after the introduction of the European carp, and the absence of aquatic vegetation may have been the result of the activities of either carp or of the native fishes.

The dominant reaction of the fishes is aided by wind and wave action, which stir up the bottom and are factors in producing high turbidity. The removal of these lakes from the effect of floods by leveeing has been another important factor in the prolongation of their existence. Physiographically, these lakes continue to exist in a rather stable condition. There is very little run-off from the surrounding lands, so that filling by in-washed sediments is relatively negligible. Rise and fall of water level is generally a result of similar changes in the level of the ground-water table or of backwater from the drainage ditches. Except for wind and wave action, the bottom is stable.

The plankton community is still that of the stream climax and abandoned stream waters. Plankters which are characteristic of the temporary pond of the later successional stage are present, but are rare or uncommon. Certain organisms have not been able to maintain themselves in the new environment. The bottom community has suffered the most. There is a notable lack of molluscs although there is evidence of a previous large population of these animals. Ephemerid nymphs are absent from the open water, and are only occasionally found in the shallow water near shore. Tubificids and midge larvae are the important constituents of the bottom fauna. In general, the community is still composed of many forms which are characteristic of the physiographic aquatic climax community. The components of the community have partially succeeded in maintaining their environment in the face of ecologic and physiographic factors that should tend to destroy it rapidly.

SUMMARY

Four lakes occupying parts of an old stream channel on the leveed floodplain of the Mississippi River near Quincy, Illinois, were selected for a study of seasonal and annual variations in the bottom fauna and plankton in relation to environmental factors.

The lakes were small and very shallow, with saucer-shaped bottoms. There were no submerged or floating aquatic plants.

Dissolved oxygen was high in the winter, except when ice covered the lakes for an unusually long time. Occasional peaks in dissolved oxygen were observed in the warmer months.

Turbidity was usually high except at times when ice covered the water.

High concentrations of carbon dioxide occurred in winter and total alkalinity was usually above 100 ppm. Lowest pH values occurred in winter, and highest values in summer, with a range of 7.2 to 8.6.

The bottom fauna was restricted in numbers of species, but deep dredges showed that a much larger assemblage of species formerly was present.

Bottom organisms, except tubificid worms, were virtually eliminated by severe reduction of dissolved oxygen during the summer, but were little affected by similar reduction during the winter.

Fish predation is indicated as an important factor in holding bottom populations at a relatively low level.

Maximum populations, or pulses, of the major net plankton groups were highly irregular in occurrence, and differed from year to year in size and seasonal appearance in each lake.

These lakes represent successional stages in the series from a climax stream community to the terrestrial community which is initiated by the stoppage of current in the original stream. The sedimentation and filling processes which normally aid the continuation of the succession are largely inoperative in this location. Wave action on the shallow bottom, and the activities of bottom-feeding fishes have maintained a partial climax condition and the lakes are at present in a condition of successional semi-stasis.

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Freshwater Ostracods From South Carolina[1]

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Appreciation is expressed to Mr. L. C. Roache and Mr. Fred H. Thompson for their help in collecting the specimens used in this study. The author acknowledges with thanks the assistance of Miss Barbara Thompson for her aid in the preparation of the drawings.

The ostracods of South Carolina have received little attention, indeed the ostracods of North America have received but scant notice. Hoff (1942) attributes the lack of ostracod studies in America to the absence of these crustaceans from most open-water plankton samples, and to the ease with which they escape from the conventional collecting apparatus. According to Pennak (1953), "Perhaps the chief reason for the general neglect of the American Ostracoda lies in the fact that they are nearly always necessarily collected in masses of débris from which they must be laboriously separated." In order to make a taxonomic study of these small, bivalved animals it is necessary to dissect them, this has doubtlessly contributed to the neglect of this group by American zoologists.

Previous reports of ostracods from South Carolina have been made by Sharpe (1908), Hoff (1944), Tressler (1947), and Ferguson (1952, 1954).

This paper is based upon approximately three hundred collections from thirty counties of South Carolina. Collections were made during the summer, fall and winter of 1953 and during the spring of 1954. Samples were taken from artificial lakes, fish ponds, rivers, back-waters of rivers, roadside ditches, etc. Of the fifteen species of ostracods reported here, seven are new to South Carolina and two are new species.

The works of Turner (1895), G. W. Müller (1912), Sars (1926, 1928), Furtos (1933, 1935, 1936), Dobbin (1941) and Hoff (1942) have been used extensively in determining synonymy and systematic details.

Methods

All collections were made with a Birge cone net of silk bolting cloth (No. 20 mesh). The net was sixteen inches in length and approximately 12.5 inches in circumference at the larger end. The net was fitted over a 4½ inch long sheet metal cylinder which was closed with one-half inch mesh wire netting. Organisms were collected by dragging the net through aquatic vegetation and along the bottom of shallow bodies of water.

Generally, samples were taken into the laboratory and poured into a Syracuse watch glass or into a Petri dish and allowed to stand for from one-half to one hour. Active forms were removed with a medicine dropper and placed in water, and 95% ethyl alcohol equal in quantity to the water was added. This method of killing ostracods facilitated dissection by producing a large number of specimens with open valves.

[1] This investigation was supported by a grant from the American Philosophical Society.

The ostracods were preserved in 85% ethyl alcohol and kept in labelled 4 dram homeopathic vials. After killing the organisms the solution was pipetted off the sample and replaced with 85% ethyl alcohol. Occasionally 95% alcohol was added to a sample without first removing the ostracods. This procedure made it necessary to perform the tedious task of separating the specimens from the débris; however, it had the distinct advantage of rapid preservation and facilitated later examination.

In the preparation of permanent whole mounts, some specimens were unstained, others were stained in 1% alcoholic solution of eosin Y. The specimens were removed from 85% ethyl alcohol, washed in 95% alcohol for one-half hour, and transferred to eosin Y. After three to five hours the stain was removed and the specimens were washed in absolute alcohol until all traces of excess stain had been removed. Microscopic mounts were prepared by placing the specimen in a drop of Canada balsam on a slide after which the valves were removed and the appendages were carefully separated. The dissected parts were covered with a No. 1 cover glass. Unstained specimens were similarly treated except for transfer to eosin Y.

Systematic Records

CYPRIDOPSIS Brady, 1867

CYPRIDOPSIS VIDUA (O. F. Müller, 1776) Brady, 1867

Remarks.—*Cypridopsis vidua* is cosmopolitan, being recorded in North America, South America, Europe and Asia. It is found in permanent bodies of still water in South Carolina during all seasons of the year; large numbers of adults and late instars were collected during the July-November period, with few individuals appearing in collections made during the winter. Immature forms were numerous in collections taken during the month of April.

Distribution.—*C. vidua* was present in samples from all counties of South Carolina from which collections were made.

POTAMOCYPRIS Brady, 1870

POTAMOCYPRIS SMARAGDINA (Vávra, 1891) Daday, 1900

Remarks.—*P. smaragdina* occurs in very small numbers in the permanent waters of South Carolina. The species apparently is not as widely distributed nor is it as abundant in South Carolina as in some of the more northern parts of the United States.

Distribution.—This species was collected from the following South Carolina counties: Calhoun, Clarendon, Chester, Dorchester, Lexington, and Orangeburg. *P. smaragdina* is also known from the states of Illinois, Louisiana, Missouri, Ohio, Tennessee, Texas, and from Bohemia, Mexico, and Switzerland.

CANDONA Baird 1845

Candona orangeburgensis n. sp.

figs. 9-15

SPECIFIC CHARACTERS: *Female.*—A *Candona* of the Compressa group. Shell elongated laterally and weakly arched; greatest height approximately six-tenths the length.

Greatest height of the shell at the posterior end. Left valve slightly longer than the right. Length 0.67 mm-0.71 mm; height 0.39 mm-0.41 mm. Anterior margin narrowly rounded; a slight sinuation between the anterior and the dorsal margins. Dorsal margin convex; the posterior margin sloping to a broadly rounded postero-ventral angle. Ventral margin with a distinct sinuation near its center. Submarginal line only slightly removed from the margin of the shell. Valves are without hairs; a few scattered puncta present on the lateral surfaces of the shell. Antennules and antennae characteristic of the genus. Maxillary palp with a broad proximal podomore and a more narrow and shorter distal one; greatest width of the proximal podomere equals one-half the length. Terminal claw of the second thoracic appendage with a length equal to the combined lengths of the penultimate and ultimate podomeres. Furca strongly developed, curved and with a length approximately ten times the least width. Terminal spine of the furca slightly longer than the subterminal one; the dorsal seta removed from the end of the ramus by the length of the seta. Terminal seta about one-half the length of the dorsal one. The genital lobe undivided, elongate and tapers to a point.

Male.—Unknown.

Remarks.—*Candona orangeburgensis* resembles *Candona acuta* Hoff (1942), but may be distinguished from the latter by the size of the valves and by the structure of the genital lobe. In *Candona acuta* the genital lobe is bluntly pointed at the posterior end, whereas this structure in *C. orangeburgensis* is sharply pointed posteriorly.

Type locality.—A roadside ditch located along U. S. highway 33 about 3 miles east of the city limits of Orangeburg, South Carolina. Adults of *C. orangeburgensis* were collected in January and in April 1954.

Type specimens.—Holotype (female) and paratype (female) are deposited in the United States National Museum (USNM 97706 and USNM 97707).

CANDONA ELLIPTICA Furtos 1933

Remarks.—A single representative of *C. elliptica* was collected from South Carolina. A late female instar was taken on January 26, 1954 from a shallow, weedy pond located in Calhoun county. The left valve measures 0.71 mm in length, and the right valve 0.69 mm. Each valve is 0.27 mm in height. The greatest height of the shell is posterior. Outer masticatory process of maxilla with two spines; the second thoracic appendage with five podomeres through the division of the antepenultimate podomere.

Distribution.—Calhoun County, South Carolina and Ohio.

CANDONA FABAEFORMIS (S. Fischer 1851)

figs. 7, 8

Remarks.—A single male specimen was collected on May 2, 1954 from a roadside ditch in Colleton County. The general morphology and the color of the shell suggest that the organism is *Candona fabaeformis* (S. Fischer 1851). Both the terminal and subterminal spines of the furca of the Colleton County specimen are smooth. The subterminal spine of the furca is pectinated and slightly different in length in the female reported by Turner (1895) from Atlanta, Georgia. Such morphological differences may be merely a matter of sexual dimorphism, or they could represent significant taxonomic differences. On the basis of the structural characteristics apparent in the present specimen, it seems to be a valid member of the species *Candona fabaeformis* (S. Fischer 1851). Subsequent investigations upon a repre-

sentative number of specimens from South Carolina may reveal other significant facts.

Distribution.—*C. fabaeformis* has been previously reported from Georgia and from Russia, and is here recorded from Colleton County, South Carolina.

CYPRICERCUS Sars 1895

CYPRICERCUS TRESSLERI Ferguson 1954

Remarks.—*C. tressleri* is the first representative of the genus to be reported from South Carolina. It is an inhabitant of temporary bodies of water. The species has been collected in large numbers during the months of January and April.

Distribution.—The species has been found in the following South Carolina counties: Berkeley, Clarendon, Florence, Lee and Orangeburg.

CYPRINOTUS Brady 1885

Cyprinotus carolinensis n. sp.
figs. 1-6

SPECIFIC CHARACTERS: *Female.*—Shell yellow with brown and purplish-black pigment. Valves elliptical above, subovate laterally, with rounded anterior and posterior margins, the anterior margin the more broadly rounded. Hyaline flange present on the anterior and posterior margins of the right valve. Dorsal margin evenly arched, ventral margin almost straight. Tubercles present on the antero-dorsal and the postero-dorsal margins of the right valve. Hairs along margins except dorsally. Numerous pore canals present. Length 1.33-1.36 mm, height 0.74-0.76 mm; greatest height in the anterior one-third of the valve. Antennule of seven podomeres with well developed natatory setae; antennae of five podomeres, natatory setae reaching only slightly beyond the middle of the end claws. Distal ends of the natatory setae of the antennae recurved. Ovaries in the postero-median part of the valve. Furcal ramus long, strongly developed; furca barely twice the length of the terminal claw; length of the ventral ramus seventeen times its least width; subterminal claw about three-fourths the length of the terminal one. Terminal claw approximately two times the length of the terminal seta.

Male.—Unknown.

Remarks.—*Cyprinotus carolinensis* resembles both *C. incongruens* (Ramdohr 1808) Turner 1895 and *C. pellucidus* Sharpe 1897. However, it differs from *C. incongruens* in the structure of the furcal ramus. Turner (1895) describes the abdominal ramus of *C. incongruens* as short, feeble, and slightly curved. Sharpe (1897) describes the natatory setae of *Cyprinotus pellucida* (*sic*) thus: "The two longer of the natatory setae of the second antennae reach but slightly beyond the terminal claws." The natatory setae of the antennae in *Cyprinotus carolinensis* barely extend beyond the middle of the claws and none reaches beyond the tips of the claws.

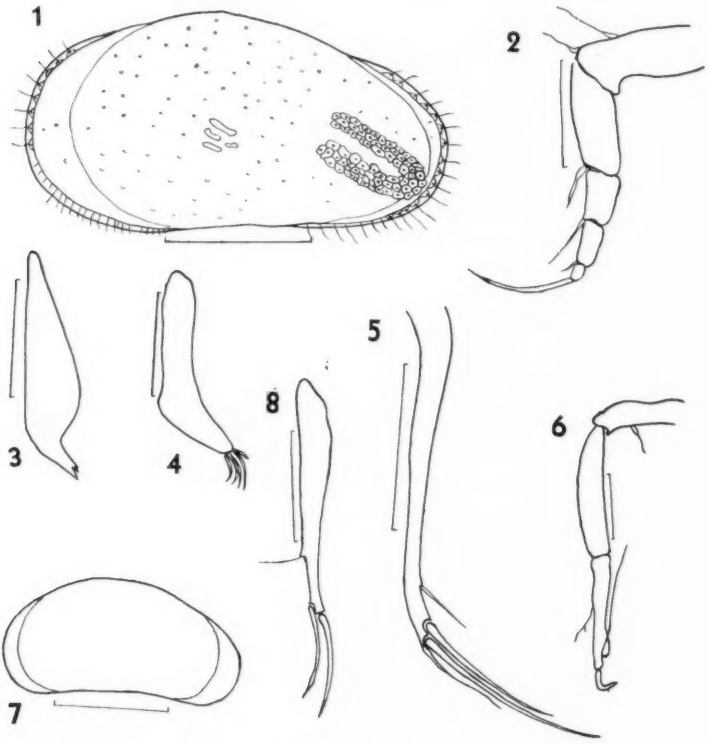
Type locality.—*C. carolinensis* was first taken from a ditch located along side U. S. Highway 33, about 5 miles east of the city of Orangeburg. Adults were collected in January, March, and April, 1954.

Type specimens.—Holotype (female) and the paratype (female) have been deposited in the United States National Museum (USNM 97708 and USNM 97709).

Distribution.—The species has been found in weedy, shallow ditches in the following South Carolina counties: Clarendon, Florence, and Orangeburg.

ILYODROMUS Sars 1894
ILYODROMUS PECTINATUS Sharpe 1909
fig. 16

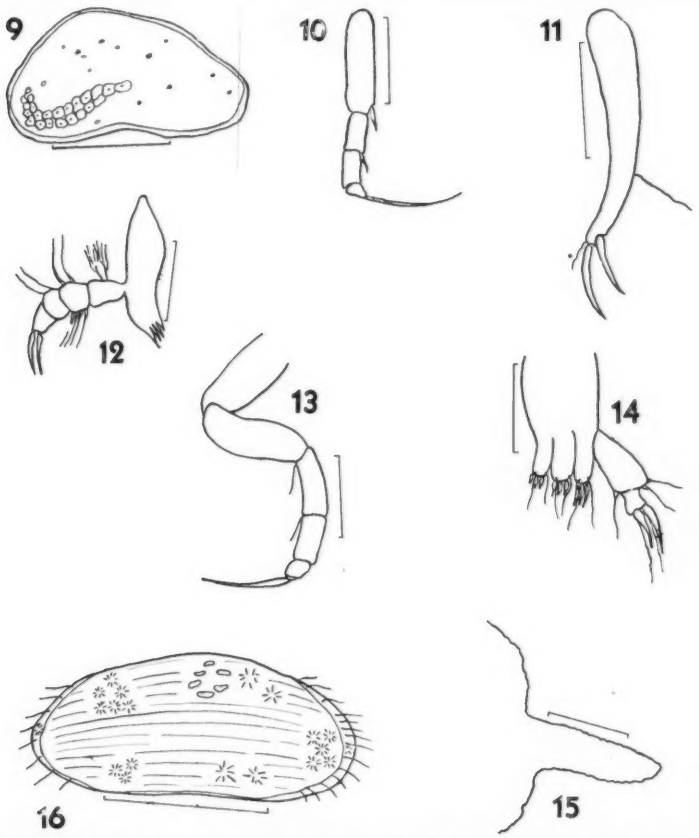
SPECIFIC CHARACTERS: *Female.*—Shell from above oval, in lateral view the anterior and posterior margins are rounded, the anterior more broadly rounded than the posterior. The dorsal margin with a slight sinuation between the highest point and the anterior margin. Submarginal line slightly removed from the margin anteriorly and posteriorly. Greatest height of the shell anterior. Ventral margin with a weak sinuation near the center. Surface of the valves with two patterns, one apparently superimposed upon the other. A series of parallel lines lying next to the outer layer of the shell with a superimposed series of circular figures each composed of a number of radiating, diagonal lines. Length of the valve 0.91 mm, height 0.47 mm. Antennules of seven podomeres and with long well developed natatory setae. Antennae strongly developed, setae of the antennae



Figs. 1-8.—1-6.—*Cyprinotus carolinensis,* ♀. 1. Mesial view of right valve (holotype). Scale: 0.47 mm; 2. Second thoracic leg (holotype). Scale: 0.01 mm; 3. Lateral view of mandible (paratype). Scale: 0.25 mm; 4. First thoracic leg (paratype). Scale: 0.1 mm; 5. Furca (holotype). Scale: 0.19 mm; 6. Third thoracic leg (holotype). Scale: .008 mm. 7, 8. *Candona fabaeformis,* ♂. 7. Mesial view of left valve. Scale: 0.45 mm; 8. Furca. Scale: 0.11 mm.

few in number, weakly developed and reach only to the middle of the claws. Length of proximal podomere of maxillary palp approximately three times the length of the distal one; distal podomere of the palp rectangular with a length twice the width. Third thoracic appendage with five podomeres through a division of the penultimate podomere. Ultimate podomere of the third thoracic appendage provided with one curved seta and a longer straight one. Furcal ramus slender and straight, with a length approximately twenty times the least width; dorsal seta absent. Terminal and subterminal spines seta-like and straight.

Remarks.—Sharpe established the species *Ilyodromus pectinatus* upon the characters of a single male collected from an undisclosed locality in South



Figs. 9-16.—9-15. *Candona orangeburgensis*, ♀. 9. Mesial view of left valve (holotype). Scale: 0.34 mm; 10. Endopodite of second thoracic leg (paratype). Scale: 0.12 mm; 11. Furca (holotype). Scale: 0.08 mm; 12. Mandible with mandibular palp (paratype). Scale: 0.10 mm; 13. Third thoracic leg (paratype). Scale: .058 mm; 14. Left maxilla with maxillary palp (paratype). Scale: .026 mm; 15. Genital lobe (holotype). Scale: .028 mm. 16. *Ilyodromus pectinatus*, ♀. Lateral view of valve. Scale: 0.46 mm.

Carolina. Consequently, characters for the female are not available in the literature since apparently this is the first record of the species since Sharpe's original description. The shell of the male is seemingly significantly longer and higher than that of the female specimens under consideration; having only females at my disposal it is not possible to determine whether the shell difference is merely a case of sexual dimorphism or whether it represents a valid species difference. However, until more detailed and extensive investigations are made, it is my opinion that the shell pattern of parallel and radiating lines and the structure of the antennae plus the form of the third thoracic appendage justify assigning these organisms to *Ilyodromus pectinatus* Sharpe 1909.

Distribution.—The author collected specimens of *I. pectinatus* from temporary bodies of water in Sumter and Florence counties during the month of January, 1954.

CYCLOCYPRIS Brady and Norman 1889

CYCLOCYPRIS SHARPEI Furtos 1933

Remarks.—*C. sharpei* was observed in small numbers in samples collected from the more northern counties of South Carolina during the summer from late June until mid-September.

Distribution.—Specimens of *C. sharpei* were collected from Chester, Greenville, and York counties. The species is also known from Ohio.

CYCLOCYPRIS FORBESI Sharpe 1897

Remarks.—A single representative of *C. forbesi* was collected by the writer in Orangeburg county in 1950. In 1952 he gave the following account of this organism:

> A single male ostracod measuring approximately 0.586 mm in length and 0.490 mm in height, with the greatest width of the shell slightly posterior to the middle was collected from a pond in which there was considerable vegetation. The shell is brownish in color and oval in shape; the ultimate podomere of the mandibular palp short; natatory setae of the antennules approximately 20X the length of the ultimate podomere. The testes are a tightly coiled mass of threads. The third thoracic leg with four podomeres and three terminal setae of unequal length; the lateral seta is long and reflexed reaching to the proximal end of the antepenultimate podomere.

Distribution.—The organism is known from Orangeburg County, and also from Illinois and Massachusetts.

CYPRIA Zenker 1854

CYPRIA INEQUIVALVA Turner 1893

Remarks.—Specimens of *C. inequivalva* were collected on May 2, 1954 from a shallow roadside ditch along U. S. Highway 17 in Charleston county. Turner (1893) in his description of the species states: "Viewed from the side the shell is subreniform, higher near the middle. It is about twice as long as high." The specimens from South Carolina are only one and one-half times as long as high. Indeed, on a basis of the measurements given by Turner (1893) for his species the length to height ratio is also approximately one and one-half to one.

Distribution.—*C. inequivalva* is reported from Charleston County; it is also known from Ohio and Georgia.

CYPRIA TURNERI Hoff 1942

Remarks.—*C. turneri* was present in a majority of the samples collected from fish ponds and standing water in roadside ditches and in open fields during the spring. In the vernal period *C. turneri* is second only to *Cypridopsis vidua* in the extent of its distribution in South Carolina. Specimens were collected from Charleston County on the coast and from Greenville County in the Piedmont section of the state. *C. turneri* was established by Hoff (1942) to accomodate American *Cypria* species that possess parallel longitudinal anastomosing lines on the shell. Previous to the publication of Hoff's monograph (1942) organisms of the genus *Cypria* with parallel and anastomosing lines on the shell were assigned to the European species *Cypria exsculpta* (S. Fischer 1855).

Distribution.—The species has been found in the following South Carolina counties: Aiken, Berkeley, Charleston, Greenville, Orangeburg, and Saluda. It has been reported under the names *C. exculpta* and *C. exsculpta* from Alabama, Delaware, Georgia, Illinois, Maine, Michigan, and under the name *Cypria elegantula* from Ohio.

CYPRIA OBESA Sharpe 1897

Remarks.—Specimens of *C. obesa* were collected from Jack's Creek located in Clarendon County on April 6, 1954 by Mr. Fred H. Thompson.

Distribution—*C. obesa* is recorded from Clarendon County, South Carolina; the species is also known from Illinois and Ohio.

CYPRIA OPHTHALMICA (Jurine 1820) Brady and Norman 1889

Remarks.—Males and females appear in approximately equal numbers in collections from South Carolina.

Distribution.—*C. ophthalmica* is known from Europe, South America, Alaska, Georgia, Tennessee, Washington, Illinois, and from Orangeburg and Saluda counties in South Carolina.

PHYSOCYPRIA Vávra 1897

PHYSOCYPRIA PUSTULOSA (Sharpe 1897) G. W. Müller 1912

Remarks.—In South Carolina specimens were taken from backwaters of rivers, farm fish ponds, and infrequently from deep roadside ditches.

Distribution.—The species has been reported from Alaska, Florida, Georgia, Illinois, Louisiana, Massachusetts, Michigan, Missouri, Mississippi, Ohio, Washington, and is reported from Aiken, Chester, Orangeburg, Saluda, and York counties in South Carolina.

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A Study of Pseudobythocypris Pediformis, a New Name for an Old Ostracod

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Fossil ostracods are prominent elements of many microfaunas and are used increasingly for stratigraphic correlation. Kesling (1952, p. 247) states that the use of ostracods as index species depends upon two factors, "(1) the determination of which particular species are 'indices' and (2) the establishment of sound principles for distinguishing a 'species.'" Paleontologists expend their major effort upon the first factor, producing studies which systematically record stratigraphic and geographic occurrences of "species." Most workers will agree that, because of relative neglect of the second factor, and because of special difficulties inherent in the study of Ostracoda, a sound taxonomic structure has not developed as rapidly as has the discovery and description of new morphologic groups. Unusually long and confusing synonymies are one result as new studies show that many early, incompletely described "species" are unreliable. Neglect of the second factor is doubtless encouraged by lack of agreement as to what is most useful and by the opinion, still held in some quarters, that paleontologists need not be concerned with "natural" species.

The writer believes that the most profitable use of ostracods in stratigraphic problems depends upon recognition of species that are as much in accord with the biologic concept of species as is possible. This becomes increasingly evident as assemblages or phylogenies are recognized as superior in index value to the traditional index species. Investigations seeking sound principles for characterization of species commonly take one of two courses: 1) complete analyses of ostracod shell structures, and 2) quantitative studies. The first method was pioneered by G. W. Müller in 1894 and finds other examples in several of Sylvester-Bradley's papers (e.g., 1941, which contains a summary to that time). The quantitative approach is newer, and Kesling (1952) should be credited with the first comprehensive application of most of the statistical concepts here applied to one species of ostracod.

Neither of these methods has received attention commensurate with the values to be achieved by ever-closer approximation of paleontologic to biologic species. The writer emphasizes the value of both methods in this study of the upper Paleozoic species originally described as *Bythocypris pediformis* Knight. Results are presented here because they show that a new genus, *Pseudobythocypris*, should be published before the ostracod portion of the *Treatise on Invertebrate Paleontology*,[1] inasmuch as its editorial policy holds that new genera should not be first cited therein. Advance publication also enables the *Treatise* author for the family Healdiidae to recognize that an

Acknowledgment is made to Mr. George M. Wilson of the Illinois Geological Survey, who supplied the collection of Exline shale fossils, and to the British Museum and U. S. National Museum for loan of type specimens. Dr. T. G. Perry criticized the manuscript.

[1] R. C. Moore, Editor. University of Kansas Press and Geological Society of America.

important element of the family consists of several species of Paleozoic age formerly assigned to genus *Bythocypris* Brady, a genus based on Recent ostracods. The scope of this paper, however, does not include restudy of all the more than 100 Paleozoic species now assigned to *Bythocypris*, although many paleontologists recognize its inadequacy for Paleozoic ostracods.

SHORT HISTORY OF BYTHOCYPRIS BRADY, 1880

The genus is based on Recent material dredged from the Atlantic by H. M. S. Challenger and studied by Brady (1880, pp. 45-49; Pl. V, fig. 1, a-l; Pl. VI, fig. 1, a-c). Brady did not then designate a type species among his three members of *Bythocypris*, but Brady and Norman (1889, p. 119) designated *B. reniformis*. They also regarded it as a synonym of the earlier *Bairdia bosquetiana* Brady (1866, p. 364), a species considered by them to consist of the young of *Bythocypris reniformis*. Although Sylvester-Bradley (1946, p. 197) showed that *B. reniformis* is the valid type species, some authors still list *Bairdia bosquentiana*.

Brady's diagnosis of the genus is concerned mostly with soft parts, and his brief statement concerning the shell is of slight paleontologic value. Re-examination of type specimens reveals that, in addition to the reniform outline in lateral view, the genus is characterized by an adductor muscle scar containing a few discrete spots and a duplicature with associated vestibule and related structures (fig. 2—1, 2). These features link *Bythocypris* with other genera in the families Bairdiidae and Cyprididae, as recognized by all students who have described *Bythocypris* from Recent material.

Although Müller (1894, Pl. 14, fig. 16) gave improved illustrations of Recent Mediterranean examples of *Bythocypris*, the difficulty of observing critical morphology in superficially similar fossil ostracods resulted in the description of more than ninety species of Paleozoic age by 1934 (Bassler and Kellett, 1934, pp. 224-235). Nearly every species must be re-examined before it can be accepted as congeneric with Recent species. The confusion in synonymy that has evolved for species of ostracods resembling the common Carboniferous ostracod, *B. pediformis* Knight, is one indication of the need for thorough examination of the species.

Some authors have used the considerable variation in an apparently single population of *B. pediformis* as a basis for introduction of many new species, though others have ascribed morphologic differences to sexual dimorphism, individual variation, or ecologic factors. Cooper (1946, pp. 55-59), doubtless impressed by differences between Recent and Paleozoic forms, transferred many species resembling *pediformis*, many of them new, to the Paleozoic genus *Coryellites* Kellett. Kellett (1935, p. 138), however, clearly distinguished *Coryellites* by its node and depression, both features that are lacking from the species which Cooper transferred to the genus. Cordell (1952, p. 100) therefore, advocated retention of many species in *Bythocypris* and made some synonyms of *B. pediformis*.

The writer agrees that many of the earlier species are not adequate in view of principles later applied to ostracods, but available evidence indicates that they are excluded from *Bythocypris* by morphologic disparities even more significant than those which Cordell used to distinguish "Bythocypris" from

Coryellites. Furthermore, assignment should not be made to the latter genus, because paucity of material does not permit study of its critical internal morphology.

Order PLATYCOPA Sars, 1866
Family HEALDIIDAE Harlton, 1933

Pseudobythocypris, gen, nov.

Type species.—*Bythocypris pediformis* Knight, 1928, (p. 326; Pl. 44, figs 3a-c). Cordell (1952, p. 100) provides a recent description and synonymy for the type species, recognizing considerable morphologic variation in accordance with the population concept applied here. Knight made no specific mention or selection of type specimens in his paper but measured and illustrated two specimens each of *B. pediformis* and its synonym *B. parallela*. These specimens, probably labelled as primary types, could not be located and possibly are lost. The writer selects four hypotypes of *B. pediformis* as follows from specimens mounted on "metatype" slides by Knight and deposited in the U. S. National Museum: USNM 133377, L = .68 mm, H = .40 mm, T = .26 mm; USNM 133378, a left valve, L = .67 mm, H = .40 mm; USNM 133379, L = .68 mm, H = .36 mm, T = .26 mm; USNM 133380, a left valve, L = .62 mm, H = .32 mm. USNM 133379-80 are selected from specimens originally identified as *parallela* which is considered to be the opposite sex.

Description.—In lateral view, carapace subovate with rounded anterior, dorsum broadly arched and mostly lacking angulation, venter nearly straight but commonly with slight posteroventral slope meeting the posterodorsal border in varying degrees of angularity. In dorsal view, lateral outlines symmetrically convex to somewhat blunt posteriorly. Moderately dimorphic. Surface of valves smooth and without sculpture. Left valve larger than and overlapping right. Contact margins consisting simply of ridge (selvage) and inner depressed shoulder (selvage groove) of left valve into which fits the sharpened edge (selvage) of right. Hinge short, simple, mostly undifferentiated and located dorsally and somewhat posteriorly. Separated calcified inner lamella with vestibule lacking. Adductor muscle scar circular with numerous closely-grouped spots.

Remarks.—*Pseudobythocypris* resembles some species of *Waylandella* (= *Harltonella* Bradfield) Coryell and Billings, 1932 but differs in lacking posterior ridges, shoulders, or spines. The new genus is distinguished from *Coryellites* (pro *Coryellina*) by absence of sculpture, and from all the most typical Bairdiidae (including *Bairdiacypris* Bradfield, 1935 and *Bythocypris* Brady) by possession of a more complex muscle scar but simpler contact margins without a separated calcified inner lamella.

Probably all, or almost all, Paleozoic species of "Bythocypris" are not properly retained therein, and the author believes the following Carboniferous species are better assigned to *Pseudobythocypris*: *Bythocypris angularis, cooki, frivola,* (?) *irregularis, mytiliformis,* and *subpediformis,* Bradfield; *B. concava* and *disparilis, Coryellites contracta, elongata, lowelli, portica,* and *scotti* Cooper; *B. kellettae, oblongata,* and *pecki* Cordell; *B. croneisi* Coryell and Rozanski; *B. palopintoensis, semicirculus,* and *texensis* Coryell and Sample; *B. clorensis* Croneis and Funkhouser; *B. lydeae* and *norrisensis Geis; B.* (?) *pyrula* Jones and Kirkby; *B. osagensis* Kellett; *B. exigua, gibbosa,* and *tenella* Kummerow; *B. amsdenensis* Morey; and *B. bisoni* Wilson. Possible Permian

representatives are *B. erectus* Harris and Worrell and *B. johnsoni* and *tumidus* Upson. Few of these species are considered synonyms by some authors, and many others are found in published synonymies.

Taxonomic position.—The platycopid margin and healdiid-cavellinid muscle scar remove *Pseudobythocypris* from the Bairdiidae or Cypridiidae and link it with the Healdiidae. Supporting evidence includes the direction of overlap (reverse of that of Cavellinidae), dimorphism (uncommon in Cypridacea), and the gradational series of forms from *Pseudobythocypris* through *Waylandella* to *Healdia* Roundy, 1926 as shown by Cooper (1946, Pls. 5, 7, 12) and others.

Bairdiocypris, which has somewhat similar morphology, is another paradoxical genus exhibiting the cyprid-bairdiid shape on one hand and healdiid finer structures on the other, and was referred by Krömmelbein (1952, pp. 321-325) to Platycopa and Healdiidae. His recommendation is not followed by some, perhaps because they think that considerable evolution or morphological variation may be allowed within the larger taxonomic units. However, most current practices generally recognize little evolution in a family group,[2] and the writer presently prefers to place *Pseudobythocypris* in the Healdiidae. The older alternative of Bairdiidae would incorporate far greater differences in that family.

MORPHOLOGY

The marginal structures, together with the adductor muscle scar, are here considered to be quite as significant as the previously all-important criterion of shape as seen primarily in lateral view. This is true especially for assignment in ranks higher than the species, although available evidence does not preclude use of muscle scars for differentiation of the broadly interpreted species of a few authors. Therefore, formal terminology should be available for adequate description of marginal structures, but the writer knows of no previous application of standard terms to each structure of the margin of convex-backed shells of the *Pseudobythocypris* type which lack "separated calcified inner lamella."

The phrase in quotes is a compromise for *duplicature* and is inserted here because of conflicting interpretations of the ostracod shell. Existing terms which can be applied to marginal grooves and ridges of *P. pediformis* are defined by some (Kesling, 1951) as applying to parts of the duplicature. Difficulty in application arises because *Pseudobythocypris* is one of many fossil ostracods whose shells lack duplicatures with vestibules as shown in the classical idealized diagram for ostracods. However, some students refer to a "fused duplicature," a condition the writer believes is not proved generally and certainly not shown in this genus. If all shells do have at least a fused duplicature, strict adherence to the classical diagram would not permit the selvage to be the principal ridge of the contact margin in the larger valve of *P.* and other platycopids.

The *selvage*, *selvage groove*, and *list* of *P. pediformis* are designated in

[2] E.g., in spite of good evidence of evolution, essentially only of the muscle scar, from a cavellinid to cytherellid condition, *Cavellina* Coryell and *Cytherella* (Jones) have come to be considered type genera of their separate Paleozoic and post-Paleozoic families, although at one time species of both were referred to *Cytherella* only.

fig. 1—7, 8 so as to make the selvage the principal contact ridge, in keeping with its most important connotation. The writer believes that corresponding designations should be made for other platycopids. Sections of *P. pediformis* (fig. 1—3, 4) show no trace of an adhesive strip, radial pore canals, or other evidence of division indicative of a fused duplicature. The hinge is short, simple, and scarcely differentiated, but its dorsal and somewhat posterior position is generally indicated by slightly greater grooving in the left valve and by slight modification in dorsal aspect of valve juncture. The adductor muscle scar as described (fig. 1—5, 6) differs greatly from Recent *Bythocypris* fig. 2—1, 2) and Paleozoic *Bairdia* (fig. 2—3).

QUANTITATIVE ANALYSIS AND ITS APPLICATION

We have said that considerable variations within populations of *Pseudobythocypris* have led some authors to recognize an excessive number of species. Other authors have thought needless splitting is the result of failure to recognize individual variation, sexual dimorphism, and molts, but few have been able to avoid recognition of some species which were later considered to be synonyms. Quantitative study of the molt series simultaneously places the three factors in their proper perspectives. Although useful, this approach is used infrequently in ostracod study because it is time-consuming and because few rocks yield sufficient numbers of large and small specimens to represent original populations.

Fig. 3 is a graph of length and height measurements of 271 specimens of all sizes, preserved as whole carapaces or as the larger left valves. They come from a two-inch zone in the Exline shale (Des Moines series of the Pennsylvanian system) in the SW¼SW¼SE¼ sec. 1, T. 8 N., R. 6 E., Peoria County, Illinois. The entire section from top to bottom is: 5 feet gray shale, 1 inch dark gray limestone, 2 inches gray shale (collected zone), 1 foot dark gray limestone with plant fossil impressions, and 10 feet shale. Only badly deformed specimens were discarded, and arbitrary decision as to what individuals constitute the species did not have to be made inasmuch as all specimens of bythocyprid appearance were acceptable in light of the quantitative treatment.

Average sizes for each molt stage, or instar, are given in table 1, together with percentage increases derived by using the preceding stage as a base. The form ratios in table 1 are pure numbers derived by height/length, thickness/length, and thickness/height. The principal dimensions are compared further as pure numbers derived by L/sum of L, H, and T; etc. Several methods for computing standard deviation, coefficient of variation, and standard error of the mean are discussed in elementary statistics texts and may be symbolized respectively by:

$$\sigma = \sqrt{\frac{\Sigma\, d^2}{N}} \qquad V = \frac{\sigma}{M} \cdot 100 \qquad \sigma M = \frac{\sigma}{\sqrt{N-1}}$$

where σ is standard deviation, d the deviation of an item from the mean, N the number of items, V the coefficient of variation, M the mean, and

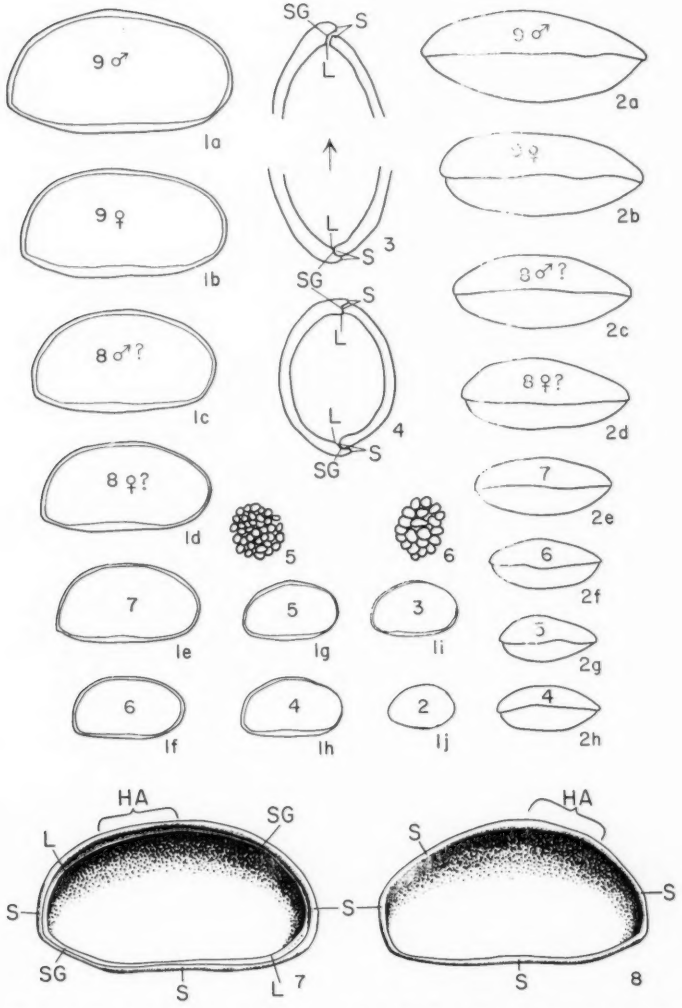

Fig. 1.—*Pseudobythocypris pediformis.*—1-4, 7, 8. *P. pediformis,* Exline shale, Penn., Peoria Co., Ill.: 1*a-j,* 2*a-h.* Right lateral and dorsal outline views respectively in molt series, instar and sex as indicated; 3, 4. Longitudinal and transverse sections; 7, 8. Left and right interior views. 5, 6, *P. pediformis,* Gimlet cyclothem, Penn., Ill.: muscle scars from exteriors of right valves (from H. W. Scott). 1*h-j,* 2*h,* 7, 8, X64; 3, 4, X75; 5, 6, approximately X115; all others X50. S—selvage, SG—selvage groove, L—list, HA—hinge area.

σM the standard error of the mean. Values for *P. pediformis* are listed in tables 4 and 5.

Number of instars.—The points in fig. 3 are divisible at once into seven or eight groups, with some question at the smaller end. Each group represents a molt stage during development and customarily is designated by a number in a series that increases with maturity. Although no more than eight stages are represented, the living ostracod probably had nine (as most modern ostracods have), and the number nine is assigned to the mature stage. This point and the apparently questionable division of instars 3 and 4 in fig. 3 are supported by application of principles implicit in Brooks' Law and by use of standard deviation.

Assuming that Brooks' Law, which is discussed later, is valid, the acceptably uniform percentage increases for length in each instar shown in table 1 are averaged to 22.8 and are used to compute lengths of 233, 189, 154, and 125 microns respectively for instars 4 to 1. Separation of the groups

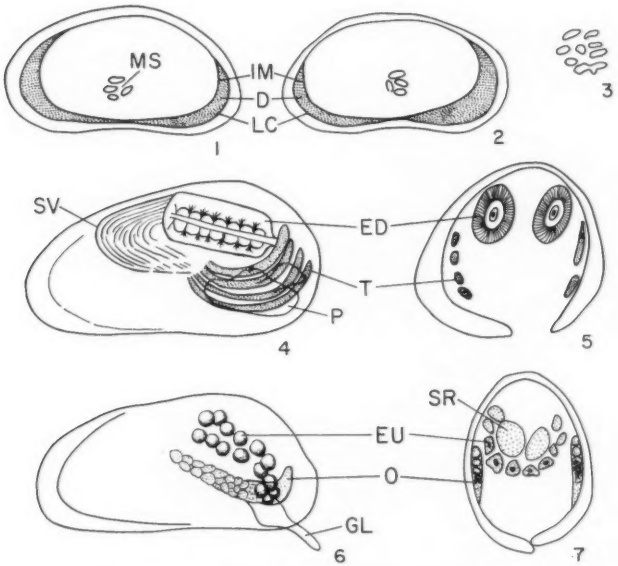

Fig. 2.—1, 2, *Bythocypris reniformis*, Recent, Atlantic, "Challenger" expedition station 122, 350 fathoms: exterior lateral outline views of left and right valves in slide 80-38 of G. S. Brady collection, British Museum, X23. 3. *Bairdia submucronata* Jones and Kirkby, Carboniferous, Woodend, Lowick, Northumberland: muscle scar from exterior of right valve, X51 (from Sylvester-Bradley). 4-7. *Candona crogmaniana* Turner, Recent, Crystal Lake Park, Urbana, Ill.: 4, 5. Left lateral and transverse (deformed) views showing genital organs of male, X28 and 41 respectively; 6, 7. Same of female. MS—muscle scar, IM—inner margin, D—duplicature, LC—line of concrescence, SV—seminal vesicle, ED—ejaculatory duct, T—testis, P—penis, SR—seminal receptacle, EU—eggs (in uterus), O—ovary, GL—genital lobe.

numbered 3 and 4 is necessary, and the mean length computed for each of them is very close to the predicted length. Assumption of nine stages for *P. pediformis* is justified further if we convert the 125 micron length of theoretical instar 1 into 19 per cent of adult length and compare it with figures for ostracods known to have nine instars (table 2). The few available data reveal that the length for this instar ranges between 15 and 25 per cent of adult length. Table 2 also shows remarkable similarity throughout the entire molt series of related species, as of species of *Cytherella* and *Cavellina*, which indicates growth characters of taxonomic value.

The proposed division into nine instars can be tested further by using the standard deviations for each instar shown in table 4. Standard deviations are useful because the mean plus and minus one standard deviation includes 68.3 per cent of the units entering into its calculation; the mean plus and minus two standard deviations includes 95.4 per cent, and so on. Using standard tables devised for any percentage and considering instar boundaries in terms of standard deviations, more than 95 per cent of the specimens clearly are assigned to instars on the basis of length; allocation of some specimens is least certain in instars 4 and 9 where 84 and 93 per cent distinctly are assignable. On the basis of height, 96 per cent of the population could not be assigned with any probability to any other instar, and 84 and 92 per cent are the lowest figures in instars 4 and 9 respectively.

The numbers of specimens recorded in fig. 3 do not show correctly the relative abundance of individuals of each molt size in the shale sample, because more time and sediment were required to find smaller carapaces.

TABLE 1.—Principal dimensions in microns for *P. pediformis* and their relationships

Item		Instar										Ave. % Inc.
		2	3	4	5	6	7	8	9MF	9F	9M	
No. Specs.	L	2	9	17	24	24	45	54	97	46	51	
	H	2	9	17	24	24	45	54	97	46	51	
	T			2	4	11	15	21	57	28	29	
Ave. L		155	193	230	286	358	440	542	656	633	674	
% Inc. L			24.5	19.2	24.3	25.0	23.0	23.1	21.0	16.8	24.4	22.8
Ave. H		103	123	138	167	208	250	300	354	328	376	
% Inc. H			19.4	12.2	21.0	24.6	20.2	20.0	17.8	9.3	25.3	19.3
Ave. T				104	138	157	186	222	262	251	272	
% Inc. T						13.8	18.5	19.4	18.0	13.1	22.5	17.4
H/L		.66	.64	.60	.58	.58	.57	.55	.54	.52	.56	
T/L					.48	.44	.42	.41	.40	.40	.40	
T/H					.83	.76	.74	.74	.74	.77	.72	
L/LHT					.484	.495	.502	.509	.516	.522	.510	
H/LHT					.283	.288	.285	.282	.278	.271	.284	
T/LHT					.234	.217	.212	.209	.206	.207	.206	

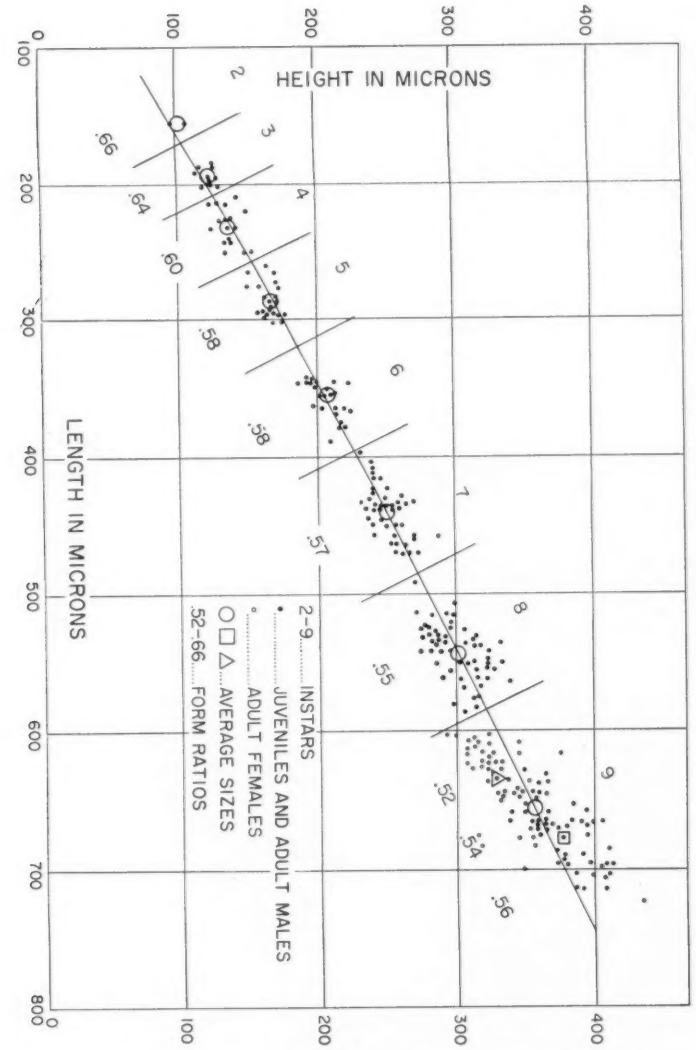

Fig. 3.—Graph showing size distribution of 271 specimens of *Pseudobythocypris pediformis*, Exline shale, Penn., Peoria Co., Ill.

However, one count in a quantity of the size grade containing specimens belonging to instars 6 to 9 recorded 10, 22, 28, and 84 individuals respectively with adult males and females in the ratio of 44 to 40.

Sexual dimorphism.—A male-female relationship in *P. pediformis* has been suspected in a few previous studies, inasmuch as an apparently single population varies between longer and narrower (less height) forms and those which are higher and more roundly arched (fig. 1—1a, b). Only Wilson (1933, p. 419) specifically designated sex and thought the two variants are male and female.

Dimorphism in *P. pediformis* is shown convincingly by the coefficients of variation in table 4. Values for immature instars are rather uniform, with no progressive trend conclusively established, but figures for the combined adults, especially in height and thickness, are the only certainly significant departures from an otherwise nearly common value. When separation by sexes is made, with uncertainty for some carapaces, coefficients return to normal

TABLE 2.—Percentage of total length attained each instar

Species and source	No. Specs.	Instar									
		Egg	1	2	3	4	5	6	7	8	9
Podocopa:											
Carbonita inflata[1]	151	(21)	25	31	36	42	48	57	69	82	100
Cypridopsis vidua[2]	500	17	21	25	31	37	44	54	68	86	100
Macrocypris succinea[3]	8		(22)	27	34	40	48	58	73	84	100
Bairdia oklahomensis[1]	94	(12)	15	18	22	27	35	46	61	80	100
B. seminalis[1]	72		(16)	20	24	30	39	50	63	81	100
Bairdoppilata sp.[1]	49			(20)	24	31	37	47	58	74	100
Fabalicypris wetumkaensis[1]	42	(15)	19	23	27	33	42	51	64	82	100
Paleocopa:											
Ctenoloculina cicatricosa[2]	68						39	50	61	75	100
Ectodemites plummeri[4]	38	(19)	23	28	35	41	51	61	73	85	100
Platycopa:											
Cavellina cavellinoides[1]	261	(20)	24	29	34	41	48	57	69	86	100
C. jejuna[5]	260	(20)	24	29	34	40	50	59	71	87	100
Cytherella bullata F[5]	110	(21)	25	29	34	42	51	59	69	82	100
Healdia cara[1]	215		(24)	29	35	42	50	58	70	83	100
Pseudobythocypris pediformis	271		(20)	24	29	35	44	55	67	83	100

F. Females ( ) Estimated

[1] Data from Shaver (1951)
[2] Data computed from Kesling (1951)
[3] Data computed from Müller (1894)
[4] Data computed from Cooper (1945)
[5] Data from Shaver (1953)

and dimorphism becomes virtually certain, though doubt remains as to whether it is sexual or parthenogenetic in origin. The variations for instar 8 in height and thickness, which are greater than in any other immature stage, suggest inconclusively the beginning of dimorphism. Shell dimorphism in immature fossil ostracods rarely has been suggested in the literature. Shaver (1953, p. 474) proposed dimorphism in at least two immature instars of Cretaceous *Cytherella bullata*. Müller (1894) and Claus (1872) recorded the appearance of genital organs in the seventh stage of Recent ostracods but did not specify clearly the effect, if any, on shell dimorphism.

Contrary to Wilson's opinion, the smaller, narrower, and more elongate adults of *P. pediformis* of the Exline sample probably are females which have been known in part as *Bythocypris parallela* or *Coryellites tomlinsonella*. In dorsal view, these adults also have the more asymmetrical outlines and the blunter posteriors (fig. 1—2a, b). Although the males are smaller and more elongate than the females in many species of ostracods, the asymmetrical female outline, with blunt posterior in dorsal view, may be a better indication of sex in dimorphic species of this type. Cordell (1952, p. 103) thought that posteriorly thinner individuals of the related species, *P. pecki*, are males, an opinion which the writer shares with regard to *P. pediformis*. However, Cordell's undesignated "narrow form" and "broad form" (pl. 20, figs. 18, 19, 22, 23) of *pecki* both have blunt posteriors in dorsal view.

The possibly aberrant, although less important, condition of greater size and dorsal arching in the male can be explained after the manner of Hessland (1949, p. 138), who followed Sars in dealing with Ordovician species. Sars (1922, p. 13) found that males of some Recent species swim actively while females are sedentary, with the result that swimming organs are best developed in the former sex. However, the fact that the greatest height in supposed males of *P. pediformis* is slightly posterior probably reflects the nature and position of the male genital organs. Paleontologists should not let the female ostracod's possession of brood pouches or egg-filled uteri obscure the fact that the male ostracod has been aptly described as a floating testicle. Fig. 2—4-7 shows how the sexual need for space is even greater in the male of the modern *Candona crogmaniana* than in the female. This ostracod also resembles *P. pediformis* in shape, and its male-female size relationships are identical with those proposed for *P. pediformis* (male larger, higher, more roundly arched). All reproductive organs in both sexes are paired, and the male of *C. crogmaniana* has eight testes (four on each side) and two each of penes, seminal vesicles, and ejaculatory ducts. The latter are large cylindrical organs located dorsally back of midpoint and on the line of greatest height, and their disproportionate space requirement suggests their relationship to higher males. Similar arrangements possibly apply to *P. pediformis*.

The nearly equal numbers of the two dimorphants of *P. pediformis* used in the study represent the true condition in the sample and are of uncertain value for recognizing either sexual or parthenogenetic reproduction or to support a particular designation of sex.

Growth relationships.—The mean sizes plotted for the separate instars on coordinate paper (fig. 3) are separated by an absolute interval increasing

with age. Hence, growth in terms of a single dimension is expressed better by a constant percentage k, than by an arithmetic amount. Because rate of growth is greater for length than for height (table 1), the growth pattern is termed *allometric* (Imbrie, 1956, p. 228). Therefore, the growth line in fig. 3 is curved. Growth lines on most published scatter diagrams for ostracods are drawn straight on coordinate paper (*isometric* growth), although many demonstrations in other animals indicate that allometric growth is the rule. Imperfections in preservation and sampling procedures probably produce departures from the inherited growth patterns so that a straight line is fitted as well as another to scatter diagrams in which allometric growth patterns are hidden. Moreover, the approach of sexual maturity or other inherent causes could reverse trends so that growth patterns may be more than *simple allometric*. This apparently is true among the males of *P. pediformis*, when height and length are the variates, and of the females in terms of height and thickness.

If the principle of a constant percentage k to express growth between molt stages nevertheless has practical validity, it can be used for taxonomic purposes and, more directly, in predicting sizes of molt stages. Fowler (1909, p. 324) first applied this principle, which he called Brooks' Law, to ostracods in terms of length. Spjeldnaes' (1951, pp. 745, 746) summarization of subsequent tests of Brooks' Law records variable conclusions regarding its validity, but the writer agrees that most denials by authors result from unsuitable samples or procedural imperfections.

Stated as a formula, Brooks' Law reads:

$$L_{(n+1)} = L_n(k+1)$$

where L_n is the length of any stage and k is a constant percentage for the species and sex. The value k for each instar in *P. pediformis* is satisfactorily uniform, with an average of 23 per cent. Thoretical and actual mean lengths in table 3 compare favorably, with significant departure only in the adult female, a departure, however, which is recorded as a cumulative effect.

Changes in shape of the carapace during growth are understood readily by reference to the bi- and trinomial form-ratios in table 1. The young of *P. pediformis* are relatively shorter, higher, and thicker than are mature individuals (fig. 1—1, 2). This growth relationship is common among ostracods and corresponds to posterior lengthening to accomodate new appendages added during growth.

Approach and attainment of sexual maturity modified the average growth relationships in *P. pediformis*. The males' rate of growth was greater, and they acquired principal dimensions each of which is greater than that of the female. Although the males' changes in shape during growth were less pronounced, they reversed the average change involving a relative decrease in height. The females grew less but became relatively more elongate. Thickness, especially in a posterior position, increased in proportion to height and is considered here to be an important character indicative of the female sex.

Because *Pseudobythocypris* has few characters which readily distinguish species, the posteroventral angulation and configuration of the venter have been used variously for taxonomic purposes and have given rise to disagree-

ment. The angulation, conspicuous in the adult Exline specimens, is present but reduced in the youngest stages; the adult posteroventral upsweep is absent from the youngest stages, as is a straight or concave venter. Can these changes in shape during ontogeny be used reliably to reconstruct an adult ancestor? Or, in *P. pediformis*, does the degree of persistence, or transience, indicate that these features have mostly a genetic or ecologic origin? The writer believes much additional information is needed in either application. Difficulty arises because a newly-hatched (from a presumably spherical or spheroidal egg) ostracod has only three pairs of appendages and lacks developed sex organs. Therefore, it must undergo metamorphosis during growth which may mask whatever morphologic features are a repetition of those of proximate adult ancestry. This point finds another example in the young molted shells of a non-sulcate adult which are slightly sulcate at the adductor muscle scar. Some students believe, therefore, that the adult ancestor was sulcate; explanation may be found also in the probability that many young ostracods lacked strong calcified shells which resisted impression at the point of adductor muscle attachment, regardless of whether the ancestor was sulcate.

Individual variation.—The spread of points in fig. 3 is a visual measure of variation in *P. pediformis*. The spread is reduced to numerical values, and among all adults the greatest variations from the means amount to 10.4 per cent for length and 22.6 for height. In adult males the figures are 8.8 per cent for length and 15.4 for height, and in females they are 7.7 and 11.9 per cent. In the early instars greatest variations uniformly approximate 9 per cent in length and 11.5 per cent in height. These percentages represent approximately one-half of the total variation in a given instar. Another method for comparison uses the coefficients of variation shown in table 4. Both analyses apparently indicate that dimensions have relatively equal variations in the separate instars, when allowance is made for dimorphism in the

TABLE 3.—Brook's Law applied to *P. pediformis*
$k = 22.8$

Instar	No. Specimens	Observed Length	Computed Length
		microns	microns
9M	51	674	
9F	46	633	
9MF	97	656	662
8	54	542	539
7	45	440	439
6	24	358	357
5	24	286	291
4	17	230	237
3	9	193*	193
2	2	155	157
1			128

* starting base

adult stage. Slight deformation of some specimens probably contributes more effectively to greater variation in height than to length.

Although Imbrie (1956, p. 228) suggested that relatively equal variations during growth are general among invertebrate fossils, his observation is not supported by the ostracod literature. Elofson (1941, pp. 378-380) recorded ranges in lengths for immature stages of many modern marine species; ranges which indicate that variations among instars are extreme. Although this contradiction of Imbrie's observation may be explained by Elofson's own statement regarding non-uniformity of his material, he nevertheless denied Brooks' Law, apparently then, without firm basis. Contrary to the results of Elofson's work, Kesling (1952, tables 19, 22) recorded coefficients of variation for the Devonian species, *Ctenoloculina cicatricosa,* and modern *Cypridopsis vidua* which indicate that variations were uniform during growth. Significantly, the coefficients computed by Kesling and that for *P. pediformis,* are each of their own magnitude. Therefore, degree of variation may be a character of taxonomic value in ostracods.

Individual variation effects considerable range in form ratios. The range of height/length in all adults of *P. pediformis* is between .46 and .61; in adult males it is between .49 and .61; in females it is .46 to .56. The range is .58 to .69 in instar 3, and values gradually decrease to .51 to .62 in instar 8. However, magnitude of range is unchanging between .10 and .12 except in a single departure to .15 in instar 4, possibly a sampling error which might appear less serious if coefficients were used rather than absolute values. Qualitatively, great ranges in form ratios and principal dimensions are accompanied by proportional ranges in thickness, thinness, elongation, shortness, dorsal arching, rounding of extremities, slope angles, and juncture angles of the four margins in lateral view.

Obviously, the practice of basing ostracod species on differences in form ratios and/or absolute size, is unsound if it is done without knowledge of variation within the species involved or without assurance that samples are adequate to reveal the extent of variations. Kellett (1933, p. 62) early noted the need for large numbers of specimens to distinguish properly intra- and interspecific variation. However, authors generally do not characterize

TABLE 4.—Standard deviations and coefficients of variation for *P. pediformis*

Instar	No. of Specs.			Length		Height		Thickness	
	L	H	T	σ	V	σ	V	σ	V
				microns		microns		microns	
9M	51	51	29	24.5	3.6	21.0	5.6	12.6	4.6
9F	46	46	28	22.6	3.6	18.1	5.5	12.1	4.8
9MF	97	97	57	31.0	4.7	31.2	8.8	16.4	6.2
8	54	54	21	20.1	3.9	17.3	5.8	12.0	5.4
7	45	45	15	18.1	4.1	12.6	5.1	9.0	4.8
6	24	24	11	13.3	3.9	11.4	5.4	7.3	4.7
5	24	24		12.3	4.2	6.6	3.9		
4	17	17		13.4	5.8	8.2	5.9		
3	9	9		7.2	3.7	5.9	4.8		

species by stating ranges in size for given numbers of specimens. Moreover, all the ostracod literature contains little or no reference to a specific number of specimens needed for understanding of variation or for reliability of numerical observations as species characters.

Numbers of specimens required for reliability.—A test of sample adequacy can be made by using standard errors of means and standard tables of probabilities. From these are computed the numbers of specimens required per instar of *P. pediformis* in order to obtain an acceptable 99 per cent probability that computed means are within arbitrary permissible ranges of the true means (table 5).

The indicated formula for computing *observed* standard errors of the means is based upon the fact that the reliability of observations made from the sample is directly proportional to the square root of the sample size, so that a fourfold increase in sample results in reduction of σM by one-half. The *required* standard errors of the means in table 5 are computed as functions of allowable 3 or 5 per cent errors and a factor of 2.576. That is, 99 out of 100 means computed would fall within the true mean plus and minus $2.576\sigma M$. Numbers of specimens are then computed as functions of the required standard errors.

The figures reveal that the quantitative observations of *P. pediformis* are reliable beyond reasonable doubt, with no more than 5 per cent error for instars 3 and 4 and with error of 3 per cent or less in instars 5 to 9. These results cannot be applied entirely to other species, each of which must be judged on its own variation. However, the writer believes that if 10 to 15 specimens represent an instar, means very likely are accurate insofar as they are affected by true variation and sample size. Some of the previous denials of Brooks' Law no doubt are correlated with sampling far short of this number. A practical application of these results also would impart greater

TABLE 5.—Numbers of specimens of *P. pediformis* required for 99 per cent probability that means are accurate within 3 or 5 per cent

Instar	Length				
	Observed	3 per cent		5 per cent	
	σ M†	Req. σ M*	N†	Req. σ M*	N†
	microns	microns		microns	
9M	3.5	7.8	(11)	13.1	(5)
9F	3.4	7.4	(11)	12.3	(4)
9MF	3.3	7.6	18	12.7	7
8	2.8	6.3	11	10.5	5
7	2.7	5.1	14	8.5	5
6	2.9	4.2	11	6.9	5
5	2.6	3.3	15	5.5	6
4	3.4	2.7	26	4.5	10
3	2.8	2.2	12	3.7	5
Ave./Instar			15		6
Req. total/7 instars			107		43
Total used this study			270		

TABLE 5.—(*continued*)

Instar	Height				
	Observed	3 per cent		5 per cent	
	σ M†	Req. σ M*	N†	Req. σ M*	N†
	microns	microns		microns	
9M	3.0	4.4	(24)	7.8	(8)
9F	2.7	3.8	(24)	6.4	(9)
9MF	3.2	4.1	59	6.9	21
8	2.4	3.5	25	5.8	10
7	1.9	2.9	19	4.8	9
6	2.4	2.4	24	4.0	9
5	1.4	1.9	13	3.2	5
4	2.1	1.6	27	2.7	10
3	2.1	1.4	19	2.4	7
Ave./Instar			29		10
Req. total/7 instars			186		70
Total used this study			270		

† N and observed σ M computed from: $\sigma M = \frac{\sigma}{\sqrt{N-1}}$

* For 99% probability, required σ M computed from: $\sigma M = \frac{.03 \text{ or } .05 \text{ M}}{2.576}$

( ) Figures not in averages or totals.

significance to the generally unqualified statements of sizes or form ratios in faunal papers.

However, little is known of the significance of mean size differences between specimens in different populations or species of the *pediformis* type which are separated by time or space. Studies in which size or other qualitative differences between species or populations are related to quantitative concepts should result in greater understanding of speciation in this difficult group.

SUMMARY

Ostracod paleontologists should exploit to full advantage two methods of study in quest of more useful taxonomy based as nearly as possible on the biologic species concept. These methods, which involve complete analysis of shell morphology and quantitative observation of molt series, are applied to the common Carboniferous ostracod, *Bythocypris pediformis* Knight. *B. pediformis* is one of possibly more than 200 species of the extravagantly artificial genus *Bythocypris* Brady, reported from Ordovician to Recent strata. Inadequacy and confusion of early concepts of *B. pediformis* and related species further indicate need for study.

Shell morphology of *B. pediformis* includes dimorphism, complex adductor muscle scars, and simple ridge-and-groove margins without duplicature. These contrast so boldly with morphology in the family Bairdiidae and the Recent

type species of *Bythocypris*, that a new genus, *Pseudobythocypris*, is introduced for 34 Carboniferous and Permian species and is transferred to Healdiidae.

Measurements of 271 specimens in a molt series of *P. pediformis* are the basis for several useful concepts: (1) An assumption of nine molt stages is supported by a graphical representation, by a growth factor of 1.23 which is used to determine theoretical means of uncertain stages, by comparisons with average lengths which several control species attain each stage, and by use of standard deviations which confirm assignment of more than 95 per cent of the specimens to stages as shown on the graph.

(2) *P. pediformis* exhibits allometric growth; a single dimension increases each molt stage by a constant percentage with some modification at sexual maturity. Measures of growth and resulting morphologic changes are useful, but difficulty arises in use of the biogenetic law for taxonomic purposes and reconstruction of ancestral morphology.

(3) Variation in size amounts to as much as 22 per cent of a mean dimension in adults of one population and effects similar variation in form ratios. Magnitude of variation is uniform during growth as shown by a nearly common coefficient of variation for each molt stage; significant departure only in the adult stage is interpreted as verification of dimorphism. Magnitude of variation and dimorphism require conservative recognition of species of this type.

(4) Computations using standard deviations and standard errors of means show that 15 and 6 specimens per instar of *P. pediformis* are required to assure a 99 per cent probability that computed mean lengths are accurate within 3 and 5 per cent respectively; 29 and 10 specimens are required for the same accuracies in height. Species of ostracods may have singular variations, possibly of taxonomic value, but 10 to 15 adult specimens would impart reliability to the statements of dimensions and form ratios commonly used to characterize a species as observed in one population.

Additional quantitative studies of species or populations which are separated by time or space, are needed for further understanding of speciation in ostracods of the *pediformis* type.

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The Vascular Flora of the Edmund Niles Huyck Preserve, New York

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The Edmund Niles Huyck Preserve is an area of considerable biological interest. It is a privately maintained wildlife preserve of 470 acres, located adjacent to Rensselaerville, Albany Co., New York, on the Helderberg Plateau about 22 miles southwest of Albany. Perhaps its most unusual feature is the maintenance of a small, biological field station, where one or more biologists have carried on field studies annually since 1939. The Preserve was formally established in 1931 in memory of Edmund Niles Huyck, a prominent eastern industrialist, by his widow, Mrs. Jessie V. A. Huyck, and friends. Since the establishment of the summer research fellowships in 1939, the results of many field studies, principally zoological, have been published by the annual research fellows.

The Preserve is centered about two bodies of water, both formed by the damming of Ten-Mile Creek. The smaller is Lincoln Pond, the larger Lake Myosotis. There is little or no level land; slopes vary from moderate to very steep in the locally famous Rensselaerville Gorge. The elevation varies from 1400 ft. to slightly more than 1700 ft. above sea level; nearby hills, not in the Preserve itself, range up to 2200 ft. Slopes facing in all directions are found and support varying vegetation types. Though the area has been protected from disturbance since about 1900, there remain a number of old fields, one of which is still cut for hay each year. The forests vary from mature hemlock-beech to many types of younger deciduous communities. Along the margins of Lincoln Pond and Lake Myosotis wet meadows, alder thickets, and even partly boggy areas are found. In addition, there is a small flora of freshwater strand plants, particularly along the shores of Lake Myosotis, where a shingle beach perhaps 20 ft. wide is annually exposed due to late summer droughts. The vegetation types have been described in other papers (Odum, 1943; Russell, 1955a, 1955b).

Because of the very diverse flora and the continued use of this area by field biologists, the need for a checklist of the flora and a herbarium for reference is very great. Some work on these has been done by a number of previous biologists, but, for the most part, it was incidental to zoological studies. Dr. Eugene P. Odum, in connection with his studies of the plant communities of the Preserve in 1939, 1940, and 1941, made a number of collections, but these apparently have been lost. In Dr. Odum's report on the vegetation (1943) he listed many species of vascular plants. Dr. W. J. Hamilton, Jr., the director of research on the Preserve, made the original survey of the Preserve in 1937 and in his typewritten report, on file in the Rensselaerville library, lists a number of vascular plants.

The list of species that follows has been prepared entirely from the collections of three investigators, Francis Harper (and his wife Jean Harper),

Ralph Smith, and the present author. These collections are all on file in the herbarium of the Preserve, located in the laboratories at Lincoln Pond. Dr. Francis Harper and his wife made several hundred collections during the growing seasons of 1949 and 1950. These were all available for the present study and had been identified in large part by Homer H. House, the former State Botanist of New York, and by Stanley J. Smith, the present Curator of the State Museum herbarium at Albany. In 1948 the research fellow, Ralph Smith, made a number of collections of vascular plants, some of which were also used in the preparation of the checklist. Finally, about 1000 collections were made during the summers of 1953 and 1954 by the present author. These, of course, included many duplicates. Sets of the majority of these collections have been deposited in the herbaria of the State University of Iowa, the University of Minnesota, and the University of Tennessee, in addition to the Preserve herbarium. Responsibility for the identification of the majority of the species listed below rests with the author. Dr. Edgar Wherry of the University of Pennsylvania kindly checked the identification of many of the ferns during a visit to the Preserve in 1954. In addition, the author received assistance in determination of difficult specimens from a number of visiting or interested botanists, notably Dr. Robert F. Thorne of the State University of Iowa and Mr. George Cooley of the Gray Herbarium.

With certain exceptions nomenclature used in the checklist follows Fernald (1950). Gleason (1952) has been followed in the treatment of the Polypodiaceae, and *Rubus* and *Crataegus* in the Rosaceae. Under the Angiosperms, the families of plants have been arranged alphabetically, as it is thought that for the majority of investigators using this checklist in the future (many of whom will be zoologists) this will make the location of families easier. A few planted species, probably incapable of maintaining themselves naturally, have been included and are indicated by asterisks. A total of 87 families are represented by 511 species in the Preserve vascular flora.

Phylum **Tracheophyta**
Subphylum **Lycopsida**

Family LYCOPODIACEAE

Lycopodium annotinum L.
L. clavatum
L. complanatum L.
var. *flabelliforme* Fern.
L. lucidulum Michx.
L. obscurum L.

Family ISOETACEAE

Isoetes engelmanni A. Br.
I. tuckermani A. Br.

Subphylum **Sphenopsida**

Family EQUISETACEAE

Equisetum arvense L.
E. fluviatile L.
E. litorale Kühl
E. sylvaticum L.

Subphylum **Pteropsida**
Class FILICINAE

Family OPHIOGLOSSACEAE

Botrychium matricariifolium A. Br.
B. virginianum (L.) Sw.

Family OSMUNDACEAE

Osmunda claytoniana L.
O. cinnamomea L.

Family POLYPODIACEAE

Adiantum pedatum L.
Asplenium trichomanes L.
Athyrium filix-femina (L.) Roth
var. *asplenioides* (Michx.) Farw.
A. filix-femina var. *Michauxii* Mett.
A. pycnocarpon (Spreng.) Tidest.

A. thelypterioides (Michx.) Desv.
Cystopteris bulbifera (L.) Bernh.
C. fragilis (L.) Bernh. var. *fragilis*
Dennstaedtia punctilobula (Michx.) Moore
Dryopteris austriaca (Jacq.) Woynar var. *intermedia* (Muhl.) Morton
D. austriaca var. *spinulosa* (Müll.) Fiori
D. cristata (L.) Gray
D. goldiana (Hook.) Gray
D. marginalis (L.) Gray
Gymnocarpium dryopteris (L.) Newm.
Matteuccia struthiopteris (L.) Todaro
Onoclea sensibilis L.
Polypodium vulgare L. var. *virginianum* (L.) Eaton
Polystichum acrostichoides (Michx.) Schott.
Pteridium aquilinum (L.) Kuhn. var. *latiusculum* (Desv.) Underw.
Thelypteris noveboracensis (L.) Nieuwl.
T. palustris Schott.
T. phegopteris (L.) Slosson

Class GYMNOSPERMAE

Family PINACEAE

Juniperus communis L. var. *depressa* Pursh
J. virginiana L. var. *crebra* Fern. & Grisc.
**Larix decidua Mill.*
**Picea abies* (L.) Karst.
**P. glauca* (Moench) Voss
**P. pungens* Engelm.
**Pinus banksiana* Lamb.
**P. resinosa* Ait.
P. strobus L.
**Pseudotsuga taxifolia* (Poir.) Britt.
**Thuja occidentalis* L.
Tsuga canadensis (L.) Carr.

Family TAXACEAE

Taxus canadensis Marsh

Class ANGIOSPERMAE

Family ACERACEAE

Acer pennsylvanicum L.
A. rubrum L.
A. saccharum Marsh
A. spicatum Lam.

Family ALISMATACEAE

Sagittaria latifolia Willd.

Family AMARANTHACEAE

Amaranthus retroflexus L.

Family ANACARDIACEAE

Rhus radicans L.
R. typhina L.

Family APOCYNACEAE

Apocynum androsaemifolium L.
A. cannabinum L.
Vinca minor L.

Family AQUIFOLIACEAE

Ilex verticillata (L.) Gray var. *verticillata*
Nemopanthus mucronata (L.) Trel.

Family ARACEAE

Arisaema triphyllum (L.) Schott.
A. stewardsonii Britt.

Family ARALIACEAE

Aralia nudicaulis L.
A. racemosa L.
Panax quinquefolius L.

Family ARISTOLOCHIACEAE

Asarum canadense L.

Family ASCLEPIADACEAE

Asclepias purpurascens L.
A. syriaca L.

Family BALSAMINACEAE

Impatiens capensis Meerb.
I. pallida Nutt.

Family BERBERIDACEAE

Berberis thunbergii DC.
B. vulgaris L.
Caulophyllum thalictroides (L.) Michx.

Family BORAGINACEAE

Echium vulgare L.
Myosotis laxa Lehm.

Family CALLITRICHACEAE

Callitriche hermaphroditica L.
C. heterophylla Pursh
C. palustris L.

Family CAMPANULACEAE

Campanula rapunculoides L.

Family CAPRIFOLIACEAE

Diervilla lonicera Mill.
Lonicera canadensis Bartr.
L. tatarica L.
Sambucus canadensis L.
S. pubens Michx.
Viburnum acerifolium L.
V. alnifolium Marsh
V. dentatum L.
V. lentago L.

Family CARYOPHYLLACEAE
Cerastium arvense L.
C. nutans Raf.
Lychnis alba Mill.
Paronychia fastigiata (Raf.) Fern.
var. *nuttalli* (Small) Fern.
Sagina procumbens L.
Saponaria officinalis L.
Silene cucubalus Wibel
Stellaria graminea L.
S. media (L.) Cyrillo

Family CELASTRACEAE
Celastrus orbiculatus Thunb.
C. scandens L.

Family CERATOPHYLLACEAE
Ceratophyllum demersum L.

Family CHENOPODIACEAE
Chenopodium album L.

Family COMPOSITAE
Achillea millefolium L.
Ambrosia artemisiifolia L.
var. *elatior* (L.) Descourtils
Anaphalis margaritacea (L.) C. B. Clarke var. *intercedens* Hara
Antennaria neglecta Greene
var. *attenuata* (Fern.) Cron.
A. plantaginifolia (L.) Richards
Anthemis cotula L.
Arctium minus (Hill) Bernh.
Aster acuminatus Michx.
A. cordifolius L.
A. divaricatus L.
A. dumosus L.
A. laevis L.
A. lateriflorus (L.) Britt.
A. macrophyllus L.
A. pilosus Willd.
A. prealtus Poir.
A. prenanthoides Muhl.
A. puniceus L.
A. simplex Willd.
Bidens cernua L.
B. frondosa L.
B. vulgata Greene
Centaurea jacea L.
C. maculosa Lam.
Chrysanthemum leucanthemum L.
var. *pinnatifidum* Lecoq & Lamotte
Cichorium intybus L.
Cirsium pumilum (Nutt.) Spreng.
C. vulgare (Savi) Tenore
Erigeron annuus (L.) Pers.
E. philadelphicus L.
E. pulchellus Michx.
E. strigosus Muhl.
Eupatorium maculatum L.
E. perfoliatum L.
E. purpureum L.
E. rugosum Houtt.
Gnaphalium uliginosum L.
Hieracium aurantiacum L.
H. florentinum All.
H. paniculatum L.
H. pilosella L.
H. pratense Tausch
H. scabrum Michx.
Inula helenium L.
Lactuca canadensis L.
Matricaria matricarioides (Less.) Porter
Prenanthes alba L.
P. altissima L.
Rudbeckia laciniata L.
R. serotina Nutt.
Senecio aureus L.
Solidago altissima L.
S. arguta Ait.
S. bicolor L.
S. caesia L.
S. flexicaulis L.
S. gigantea Ait. var. *leiophylla* Fern.
S. graminifolia (L.) Salisb.
S. juncea Ait.
S. nemoralis Ait var. *nemoralis*
S. rugosa Ait.
Sonchus asper (L.) Hill
S. oleraceus L.
Tanacetum vulgare L.
Taraxacum officinale Weber
Tragopogon pratensis L.
Tussilago farfara L.

Family CORNACEAE
Cornus alternifolia L. f.
C. canadensis L.
C. racemosa Lam.
C. rugosa Lam.
C. stolonifera Michx.

Family CORYLACEAE
Alnus rugosa (Du Roi) Spreng.
Betula lenta L.
B. lutea Michx. f. (incl. var. *macrolepis* Fern.)
B. papyrifera Marsh
Carpinus caroliniana Walt.
var. *virginiana* (Marsh.) Fern.
Ostrya virginiana (Mill.) K. Koch

Family CRASSULACEAE
Sedum purpureum (L.) Link

Family CRUCIFERAE
Barbarea vulgaris R. Br.
Brassica nigra (L.) Koch
Capsella bursa-pastoris (L.) Medic.
Cardamine pennsylvanica Muhl.
Dentaria diphylla Michx.
Erysimum cheiranthoides L.

Lepidium campestre (L.) R. Br.
L. virginicum L.
Rorippa islandica (Oeder) Borbás
var. *islandica*
R. islandica
var. *fernaldiana* Butt. & Abbe
Sisymbrium officinale (L.) Scop.
var. *leiocarpum* DC.

Family CYPERACEAE
Carex arctata Boott
C. bromoides Schkuhr.
C. communis Bailey
C. crinita Lam. var. *gynandra* (Schwein.) Schwein. & Torr.
C. lupulina Muhl.
C. pedunculata Muhl.
C. plantaginea Lam.
C. prasina Wahlenb.
C. rosea Schkuhr.
C. scoparia Schkuhr.
C. torta Boott
C. tribuloides Wahlenb.
Eleocharis acicularis (L.) R. & S.
E. obtusa (Willd.) Schultes.
E. palustris (L.) R. & S.
var. *major* Sonder
Scirpus pedicellatus Fern.

Family ERICACEAE
Vaccinium angustifolium Ait.
var. *laevifolium* House

Family EUPHORBIACEAE
Acalypha rhomboidea Raf.
Euphorbia vermiculata Raf.

Family FAGACEAE
Fagus grandifolia Ehrh.
Quercus rubra L.
var. *borealis* (Michx. f.) Farw.

Family FUMARIACEAE
Dicentra canadensis (Goldie) Walp.

Family GENTIANACEAE
Gentiana andrewsii Griseb.

Family GERANIACEAE
Geranium robertianum L.

Family GRAMINEAE
Agropyron repens (L.) Beauv.
Agrostis hyemalis (Walt.) BSP.
var. *hyemalis*
A. hyemalis var. *tenuis* (Tuckerm.) Gl.
A. perennans (Walt.) Tuckerm.
A. stolonifera L.
var. *major* (Gaud.) Farw.
A. tenuis Sibth.
Anthoxanthum odoratum L.
Brachyeletrum erectum (Schreb.) Beauv.
Bromus inermis Leyss.
B. secalinus L.
Cinna arundinacea L.
C. latifolia (Trev.) Griseb.
Danthonia spicata (L.) Beauv.
Echinochloa crusgalli (L.) Beauv.
E. pungens (Poir.) Rydb.
Eragrostis hypnoides (Lam.) BSP.
Festuca obtusa Spreng.
F. rubra L.
Glyceria borealis (Nash) Batchelder
G. canadensis (Michx.) Trin.
G. grandis S. Wats.
G. melicaria (Michx.) Hubbard
G. pallida (Torr.) Trin.
var. *fernaldii* Hitchc.
G. striata (Lam.) Hitchc.
Leersia oryzoides (L.) Sw.
Muhlenbergia frondosa (Poir.) Fern.
Panicum capillare L. var. *agreste* Gatt.
P. lanuginosum Ell.
P. subvillosum Ashe
Phleum pratense L.
Poa alsodes Gray
P. annua L.
P. compressa L.
P. pratensis L.
P. trivialis L.
Setaria glauca (L.) Beauv.

Family GUTTIFERAE
Hypericum boreale (Britt.) Bickn.
H. ellipticum Hook.
H. mutilum L.
H. perforatum L.

Family HAMAMELIDACEAE
Hamamelis virginiana L.

Family HYDROCHARITACEAE
Elodea canadensis Michx.
Vallisneria americana Michx.

Family HYDROPHYLLACEAE
Hydrophyllum virginianum L.

Family IRIDACEAE
Iris versicolor L.
Sisyrinchium angustifolium Mill.
S. mucronatum Michx.

Family JUGLANDACEAE
Carya cordiformis (Wang.) K. Koch
C. ovata (Mill.) K. Koch
Juglans cinerea L.

Family JUNCACEAE
Juncus effusus L. var. *effusus*
J. effusus var. *compactus* Lej. & Court.
J. tenuis Willd.
Luzula campestris (L.) DC.

Family LABIATAE
Collinsonia canadensis L.
Galeopsis tetrahit L.
Glechoma hederacea L.
Hedeoma pulegioides (L.) Pers.
Leonurus cardiaca L.
Lycopus americanus Muhl.
L. uniflorus Michx.
L. virginicus L.
Mentha arvensis L.
var. *villosa* (Benth.) S. R. Stewart
M. gentilis L.
M. piperita L.
M. spicata L.
Nepeta cataria L.
Origanum vulgare L.
Prunella vulgaris L. var. *vulgaris*
P. vulgaris var. *lanceolata* (Bart.) Fern.
Pycnanthemum tenuifolium Schrad.
Satureja vulgaris (L.) Fritsch
var. *neogaea* Fern.
Scutellaria epilobiifolia A. Hamilton
S. lateriflora L.

Family LAURACEAE
Lindera benzoin (L.) Blume

Family LEGUMINOSAE
Amphicarpa bracteata (L.) Fern.
Lotus corniculatus L.
Medicago lupulina L.
Melilotus alba Desr.
M. officinalis (L.) Lam.
Robinia pseudo-acacia L.
Trifolium agrarium L.
T. arvense L.
T. hybridum L.
T. pratense L.
T. repens L.
Vicia angustifolia Reichard
V. cracca L.
V. tetrasperma (L.) Moench

Family LEMNACEAE
Lemna minor L.
Spirodela polyrhiza (L.) Schleid.

Family LILIACEAE
Allium tricoccum Ait.
Clintonia borealis (Ait.) Raf.
Erythronium americanum Ker.
Maianthemum canadense Desf.
var. *canadense*
Medeola virginiana L.
Polygonatum pubescens (Willd.) Pursh
Smilacina racemosa (L.) Desf.
Streptopus amplexifolius (L.) DC.
var. *americanus* Schultes
Trillium erectum L.
T. undulatum Willd.
Uvularia grandiflora Sm.
U. sessilifolia L.
Veratrum viride Ait.

Family LOBELIACEAE
Lobelia inflata L.

Family LYTHRACEAE
Lythrum salicaria L.
var. *tomentosum* (Mill.) DC.

Family MALVACEAE
Malva moschata L.
M. neglecta Wallr.

Family NAJADACEAE
Najas flexilis (Willd.)
Rostk. & Schmidt

Family OLEACEAE
Fraxinus americana L.
F. nigra Marsh.
F. pennsylvanica Marsh.
var. *subintegerrima* (Vahl) Fern.

Family ONAGRACEAE
Circaea alpina L.
C. quadrisulcata (Maxim. Franch. & Sav.) var. *canadensis* (L.) Hara
Epilobium coloratum Biehler
E. hirsutum L.
E. strictum Muhl.
Ludwigia palustris (L.) Ell.
var. *americana* (DC.) Fern. & Grisc.
Oenothera biennis L.
O. perennis L.

Family ORCHIDACEAE
Corallorhiza maculata Raf.
Epipactis helleborine (L.) Crantz
Habenaria lacera (Michx.) Lodd.
H. orbiculata (Pursh) Torr.
H. psycodes (L.) Spreng. var. *psycodes*

Family OROBANCHACEAE
Epifagus virginiana (L.) Bart.
Orobanche uniflora L.

Family OXALIDACEAE
Oxalis europaea Jord.
O. montana Raf.

Family PAPAVERACEAE
Chelidonium majus L.

Family PHRYMACEAE
Phryma leptostachya L.

Family PLANTAGINACEAE
Plantago lanceolata L.
P. major L.
P. rugelii Dcne.

Family POLYGALACEAE
Polygala sanguinea L.

Family POLYGONACEAE
Rumex acetosella L.
R. crispus L.
R. domesticus Hartm.
R. obtusifolius L.
Polygonum arifolium L.
P. aviculare L.
P. convolvulus L.
P. erectum L.
P. hydropiper L.
P. lapathifolium L.
P. pennsylvanicum L. var. *pennsylvanicum*
P. pennsylvanicum var. *laevigatum* Fern.
P. persicaria L.
P. punctatum Ell.
P. sagittatum L.
P. tenue Michx.

Family PORTULACACEAE
Claytonia caroliniana Michx.
Portulaca oleracea L.

Family PRIMULACEAE
Lysimachia ciliata L.
L. nummularia L.
L. quadrifolia L.
L. terrestris (L.) BSP.
L. thyrsiflora L.
Trientalis borealis Raf.

Family PYROLACEAE
Monotropa hypopithys L.
M. uniflora L.
Pyrola elliptica Nutt.

Family RANUNCULACEAE
Actaea pachypoda Ell.
A. rubra (Ait.) Willd.
Anemone virginiana L.
Aquilegia vulgaris L.
Clematis virginiana L.
Coptis groenlandica (Oeder) Fern.
Hepatica acutiloba DC.
Ranunculus abortivus L.
R. acris L.
R. bulbosus L.
R. pennsylvanicus L. f.
R. recurvatus Poir.
R. septentrionalis Poir.
Thalictrum dioicum L.
T. polygamum Muhl.

Family ROSACEAE
Agrimonia gryposepala Wallr.
A. striata Michx.
Amelanchier arborea (Michx. f.) Fern.
A. laevis Wieg.
Crataegus brainerdi Sarg.
C. crus-galli L.
C. macrosperma Ashe
C. monogyna Jacq.
C. pruinosa (Wendl.) K. Koch
Filipendula ulmaria (L.) Maxim.
Fragaria vesca L. var. *americana* Porter
F. virginiana Duchesne
Geum aleppicum Jacq.
var. *strictum* (Ait.) Fern.
G. canadense Jacq.
G. laciniatum Murr.
G. rivale L.
Potentilla argentea L.
P. norvegica L.
P. recta L.
P. simplex Michx.
Prunus americana Marsh.
P. avium L.
P. pennsylvanica L. f.
P. serotina Ehrh.
P. virginiana L.
**Pyrus decora* (Sarg.) Hyland
P. malus L.
Rubus allegheniensis Porter
R. odoratus L.
R. orarius Blanchard
R. pubescens Raf.
R. strigosus Michx.
Spiraea latifolia (Ait.) Borkh.
S. tomentosa L.
Waldsteinia fragarioides
(Michx.) Tratt.

Family RUBIACEAE
Galium asprellum Michx.
G. boreale L. var. *intermedium* DC.
G. mollugo L.
G. obtusum Bigel.
G. palustre L.
G. tinctorium L.
G. trifidum L.
G. triflorum Michx.
G. verum L.
Mitchella repens L.

Family SALICACEAE
Populus balsamifera L.
P. deltoides Marsh.
P. grandidentata Michx.
P. tremuloides Michx.
Salix alba L.
S. babylonica L.
S. bebbiana Sarg.
S. discolor Muhl.
S. humilis Marsh.
S. lucida Muhl.
S. nigra Marsh.
S. sericea Marsh.

Family SAXIFRAGACEAE
Chrysosplenium americanum Schwein.
Mitella diphylla L.
Penthorum sedoides L.
Ribes cynosbati L.
R. sativum Syme
Saxifraga pennsylvanica L.
S. virginiensis Michx.
Tiarella cordifolia L.

Family SCROPHULARIACEAE
Chelone glabra L.
Gratiola neglecta Torr.
Linaria vulgaris Hill.
Lindernia dubia (L.) Pennell
Mimulus ringens L.
Penstemon digitalis Nutt.
Verbascum thapsus L.
Veronica americana (Raf.) Schwein.
V. arvensis L.
V. chamaedrys L.
V. officinalis L.
V. scutellata L.
V. serpyllifolia L.

Family SOLANACEAE
Solanum dulcamara L.

Family SPARGANIACEAE
Sparganium americanum Nutt.
S. chlorocarpum Rydb.

Family TILIACEAE
Tilia americana L.

Family TYPHACEAE
Typha latifolia L.

Family ULMACEAE
Ulmus americana L.

Family UMBELLIFERAE
Angelica atropurpurea L.
Carum carvi L.
Cicuta bulbifera L.
Conium maculatum L.
Cryptotaenia canadensis (L.) DC.
Daucus carota L.
Hydrocotyle americana L.
Osmorhiza claytoni (Michx.) C. B. Clarke
Pastinaca sativa L.
Sanicula marilandica L.
Sium suave Walt.
Zizia aurea (L.) W. D. J. Koch

Family URTICACEAE
Laportea canadensis (L.) Wedd.
Pilea pumila (L.) Gray
Urtica dioica L.
U. procera Muhl.

Family VERBENACEAE
Verbena hastata L.
V. urticifolia L.

Family VIOLACEAE
Viola blanda Willd.
V. canadensis L.
V. conspersa Reichenb.
V. cucullata Ait.
V. fimbriatula Sm.
V. incognita Brainerd
V. macloskeyi F. E. Lloyd subsp. *pallens* (Banks) M. S. Baker
V. pennsylvanica Michx.
V. pubescens Ait.
V. renifolia Gray
V. rotundifolia Michx.
V. selkirkii Pursh
V. septentrionalis Greene

Family VITACEAE
Parthenocissus inserta (Kerner) K. Fritsch
P. quinquefolia (L.) Planch.
Vitis riparia Michx.

Family ZOSTERACEAE
Potamogeton epihydrus Raf.
P. gramineus L.
P. perfoliatus L. var. *bupleuroides* (Fern.) Farw.
P. vaseyi Robbins

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Vascular Plants of Grand Teton National Park

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Grand Teton National Park is situated in northwestern Wyoming, a few miles south of Yellowstone National Park. The park embraces 484 square miles and occupies the greatest portion of Teton County. Much of the park is true wilderness, including the 40 mile long Teton Mountain Range and the slightly longer valley trough—Jackson Hole.

Topography

In the rugged mountainous country several glacier-clad peaks tower above 12,000 feet. These drop off into tremendous U-shaped canyons which tell a story of the master carvers—the many glaciers of the past. The valley has been a meeting place for these glaciers and an outwash plain for rivers of the interglacial periods. Moraines, pot holes, and river terraces are conspicuous marks left by these gigantic forces of erosion. Piedmont lakes, impounded behind tree covered terminal and lateral moraines, are found at the mouths of the major canyons. In the higher altitudes innumerable smaller lakes again reflect the forces of more recent and less vigorous glaciers. The highest peak of the range, Grand Teton, (13,766 feet) rises 7,000 feet above the valley floor.

Climate of the Valley

By referring to the weather records kept at the town of Moran since 1911,[1] a picture of atmospheric severity is revealed. The valley has always had long, cold winters with deep, drifting snow, a low mean annual temperature (34.4° F) and a short growing season of approximately 60 frost free days. The mean annual precipitation is slightly under 22 inches, and much of this comes in the form of snow (mean annual snowfall is 136.9 inches). No temperature or precipitation data are available for the range.

Vegetation

Everywhere within the park there are sharp lines of separation between different types of vegetation. The most conspicuous separations are a result of the path of the Snake River and its tributaries cutting into the bottom of the valley floor, the morainal deposits of at least three glacial periods, and altitudinal changes of the entire range. Variations in precipitation, soil and air temperature, wind, duration of growing season, and exposure are visibly manifested by the various plant communities.

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[1] Reed, J. F. 1952—Vegetation of Jackson Hole Wildlife Park, Wyoming. Amer. Midl. Nat. 48(3):700-729.

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The staff of the University of Wyoming's Jackson Hole Biological Research Station aided greatly by permitting free access to their library and herbarium.

Five major plant areas are here recognized. A brief description of each area is given and the most characteristic plants are listed. Such indicator species are not confined to just one area but reach maximum growth or frequency within it.

COTTONWOOD-BLUE SPRUCE STREAMSIDE FOREST

This type of plant area occupies the banks of the major streams of the valley and the river bottom of the Snake River. Thus the paths of permanent streams and the river are traceable throughout the valley by trails of green in the grayness of the sagebrush desert. The narrow-leaf cottonwood (*Populus angustifolia*) and blue spruce (*Picea pungens*) are the major dominants, but the balsam poplar (*Populus balsamifera*) also shares dominance in some regions. Lodgepole pine (*Pinus contorta*) and aspen (*Populus tremuloides*) are occasionally found here but neither is an important species. Various species of willows are the chief components as far as shrubs are concerned. Other common shrubs include the rose (*Rosa woodsii*), serviceberry (*Amelanchier alnifolia*), and buffaloberry (*Shepherdia canadensis*).

SAGEBRUSH DESERT

An open, shrub growth covers many square miles of outwash plain and old river terraces. It is clearly the most extensive vegetation in the valley. The most characteristic plant is the big sagebrush (*Artemisia tridentata*), however several other species of shrubs are important components of this area, including snowberry (*Symphoricarpos* spp.), bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothamnus nauseosus*).

Some of the more common herbs which can be found here are various species of *Erigeron, Aster* spp., *Taraxacum officinale, Balsamorrhiza sagittata, Antennaria* spp., *Potentilla* spp., and *Gilia aggregata.* Grasses of many genera complete the ground cover under the shrubs.

LODGEPOLE PINE-ASPEN-ALPINE FIR FOREST

Terminal and lateral moraines of the valley trough are especially prominent because of this forest which is in sharp contrast to the extensive sagebrush flats. Lodgepole pine (*Pinus contorta*) is dominant as the result of fires which occurred approximately seventy-five years ago. Alpine fir (*Abies lasiocarpa* may eventually replace the lodgepole pine as the climax forest develops. Aspen stands (*Populus tremuloides*) are rather irregular, occurring mainly on the steep slopes of the moraines.

The most conspicuous shrubs are mountain ash (*Sorbus scopulina*), low bush huckleberry (*Vaccinium scoparium*), mountain lover (*Pachystima myrsinites*), twinberry honeysuckle (*Lonicera involucrata*), and rusty menziesia (*Menziesia ferruginea*).

Herbaceous plants of this forest include *Arnica cordifolia, Helianthella quinquenervis, Epilobium angustifolium, Geranium nervosum, Viola* spp., and *Lupinus* spp.

ENGELMANN SPRUCE-ALPINE FIR-WHITE BARK PINE FOREST

This forest community occupies the steep mountain slopes and canyons

from 6,900 feet to 10,000 feet, and is composed principally of three coniferous dominants—Engelmann spruce (*Picea engelmanni*), alpine fir (*Abies lasiocarpa*) and white bark pine (*Pinus albicaulis*). Douglas fir (*Pseudotsuga menziesii*) and limber pine (*Pinus flexilis*) are also characteristic of lower portions of this forest.

Common shrubby forms are Western thimbleberry (*Rubus parviflorus*), Utah honeysuckle (*Lonicera utahensis*), spiraea (*Spiraea densiflora*), Western black currant (*Ribes petiolare*), snowbrush ceanothus (*Ceanothus velutinus*), and high bush huckleberry (*Vaccinium membranaceum*). Along the streams of this plant area are found such colorful herbs as *Aquilegia caerulea, Mimulus lewisii, Aconitum columbianum* and *Castilleja* spp.

ALPINE

The alpine area with its prevailing low temperatures and exceedingly short growing season is located between 10,000 feet and 13,500 feet. Low annuals and perennials related to arctic species are represented in this barren tundra.

The rocky talus slopes and wind swept ridges are habitats for clumps of *Silene acaulis, Geum rossii, Polemonium viscosum, Chaenactis alpina,* and *Epilobium latifolium.*

Near the summits of the higher peaks are found scattered colonies of *Smelowskia calycina, Eritrichium elongatum,* and *Saxifraga oppositifolia.*

Alpine lakes and streams are surrounded by a great variety of plants. *Primula parryi, Salix arctica, Anemone globosa,* and *Phyllodoce empetriformis* are species of these moist situations.

HISTORY OF PLANT COLLECTING IN JACKSON HOLE AND GRAND TETON NATIONAL PARK

Louis Williams is the first person who seriously collected plants of the valley and the range for the park herbarium and for distribution to other herbaria. His collections began in 1932 and continued through the summers of 1933 and 1934. Virginia and Harold Bailey spent considerable time collecting in the high country of the park during the summer of 1935, but none of their material has ever been mounted for the park herbarium. Frank W. Pierson contributed during the summer of 1936. With the establishment of the Jackson Hole Wildlife Park in 1947, (just one mile east of the Jackson Lake Dam) John F. Reed, an ecologist from the University of Wyoming, embarked on a thorough collecting program within the 1,400 acres of that area. By 1950, these specimens were incorporated into a herbarium which is available at the University of Wyoming's Jackson Hole Biological Research Station, Moran, Wyoming. Additional specimens are being added by the station's staff each year.

In the summer of 1950, the writer entered the Park Service as a seasonal ranger-naturalist, and for the past eight summers has actively collected in as many areas of the park as possible. All of these plants are on file at the park herbarium and partial sets are also included in the Intermountain Herbarium at Utah State University, Logan, Utah.

EXPLANATIONS AND ARRANGEMENT OF THE FLORA

The annotated catalogue lists 605 species of vascular plants which have been collected in Grand Teton National Park. These species represent 293 genera in 73 families. Six families and 17 species are ferns and fern allies, while two families and eight species are gymnosperms.

In the following list of plants an attempt has been made to include the abundance of each species and its usual habitat. Rare, infrequent, frequent, common and abundant are the relative terms used. The specific listing of families follows the phylogenetic scheme of most taxonomic manuals. Genera and species are arranged alphabetically. In most instances one or two collector's initials and numbers are given. The following abbreviations apply: JFR—John F. Reed, HEB—Harold E. Bailey, FWP—Frank W. Pierson, LW—Louis Williams, WGS—William G. Solheim, and RJS—Richard J. Shaw.

Catalogue of Vascular Plants of Grand Teton National Park

OPHIOGLOSSACEAE

Botrychium coulteri Underw.—Rare near outlet of Jenny Lake (LW 1695).

POLYPODIACEAE

Adiantum pedatum L.—Frequent along stream on south facing slope two miles up Waterfall Canyon (RJS 1000).

Athyrium filix-femina (L.) Roth.—Frequent along stream draining into the valley lakes, also up to 7500 ft. in the major canyons (RJS 1003).

Cheilanthes siliquosa Maxon.—Frequent in rocks on the south facing slope of Waterfall Canyon, 7500 ft. (RJS 1001).

Cryptogramma acrostichoides R. Br.—Frequent in the lower portions of the major canyons, including Avalanche and Cascade Canyons (RJS 694 & 939).

Cystopteris fragilis (L.) Bernh.—Infrequent in rock crevices in Cascade Canyon and the slopes of Symmetry Spire (RJS 973, JFR 3001).

Dryopteris disjuncta (Ledeb.) Morton.—Frequent in wet areas at the mouths of the major canyons (RJS 1002, LW 1680).

Polystichum lonchitis (L.) Roth.—Frequent in rocks in major canyons up to 9000 ft. (RJS 966, LW, 1752).

Pteridium aquilinum (L.) Kuhn. var. *pubescens* Underw.—Frequent on talus slopes of the major canyons up to about 8000 ft., including Waterfall Canyon (RJS 999, LW 1323).

Woodsia scopulina D. C. Eaton.—Frequent in talus slopes up to 8000 ft., major canyons (RJS 551, JFR 2998).

MARSILEACEAE

Marsilea vestita Hook and Grey.—Locally frequent in small pond just north of the Square "G" Ranch (RJS 1020).

EQUISETACEAE

Equisetum arvense L.—Locally common in wet areas along the trail on the west side of Jenny Lake (RJS 931, JFR 891).

E. hyemale L. Infrequent in the Wildlife Range (JFR 2905).

E. laevigatum A. Br.—Common in the sedge meadow of the Wildlife Range (JFR 1404).

E. variegatum Schleich.—Infrequent in the Wildlife Range (JFR 2206).

LYCOPODIACEAE

Lycopodium annotinum L.—Rare on the southwest shore of Leigh Lake near water's edge, 1½ miles from bridge separating String and Leigh Lakes, 6800 ft. (RJS 879).

SELAGINELLACEAE

Selaginella densa Rydb.—Common in the sagebrush flats (RJS 1008, LW 1395).

PINACEAE

Abies lasiocarpa (Hook.) Nutt.—Abundant on moraines and mountains up to timberline (RJS).

Picea engelmanni Parry ex Engelm.—Common on the west shores of the valley lakes and throughout the canyons up to about 8500 ft. (RJS).

P. pungens Engelm.—Abundant along Snake River (RJS).

Pinus albicaulis Engelm.—Common in the canyons above 8000 ft. (RJS).

P. contorta Dougl.—Abundant throughout the valley (RJS).

P. flexilis James.—Frequent on the moraines (RJS).

Pseudotsuga menziesii (Mirb.) Franco.—Common on the moraines and in the canyons below 8500 ft. (RJS).

CUPRESSACEAE

Juniperus communis L. var. *montana* Ait.—Frequent on the east shore of String Lake, mouth of Cascade Canyon, and Wildlife Range (RJS).

TYPHACEAE

Typha latifolia L.—Locally common in wet areas of the Wildlife Range (RJS).

SPARGANIACEAE

Sparganium angustifolium Michx.—Infrequent in beaver ponds along the Snake River (RJS 714, 959).

NAJADACEAE

Potamogeton filiformis Pers.—Common in ponds of the Wildlife Range (JFR).

P. foliosus Raf.—Submerged in Swan Lake (WGS 4070).

P. lucens L.—Common in the ponds of the Wildlife Range (JFR).

P. natans L.—Swan Lake (WGS 4071).

P. perfoliatus L.—Infrequent in running water in Wildlife Range (JFR).

P. pusillus L.—Frequent in pools and streams of the Wildlife Range (JFR).

P. richardsonii (Benn.) Rydb.—Common in ponds of the Wildlife Range (JFR).

P. alpinus Balbis var. *tenuifolius* (Raf.) Ogden.—Frequent in ponds of the Wildlife Range (JFR).

P. zosteriformis Fern.—Submerged in Swan Lake (WGS 4067).

ALISMACEAE

Sagittaria cuneata Sheld.—Frequent on the southeast shore of Two Ocean Lake, also in pools around Jackson Lake (RJS 949, LW 1624).

GRAMINEAE

Agropyron albicans Scribn. & Smith.—Infrequent in the sagebrush flats (JFR).

A. dasystachyum (Hook.) Scribn.—Infrequent in sagebrush areas of the Wildlife Range (JFR 1415).

A. subsecundum (Link.) Hitchc.—Frequent in the streamside forest of the Wildlife Range (JFR).

A. trachycaulum (Link.) Malte.—Frequent along the Snake River (JFR 1414, RJS 947).

Agrostis alba L.—Frequent, moist aspen groves of the Wildlife Range (JFR 1241).

A. exarata Trin.—Frequent in waste places of the Wildlife Range (JFR 1010).

A. scabra Willd.—Common in waste places throughout the valley (JFR 1426).

A. humilis Vasey.—Amphitheater Lake (LW 1480).

Alopecurus aequalis Sobol.—Frequent on mud and wet sand in Pacific Creek area (JFR 907).

Beckmannia syzigachne (Steud.) Fern.—Infrequent near margin of Pacific Creek bed (JFR 908).

Bromus anomalus Rupr.—Frequent along Snake River bottom (JFR 1345).

B. carinatus H. & A.—Common in the sagebrush flats and Snake River bottoms (RJS 942, JFR 1347).

B. ciliatus L.—Common along the Snake River (RJS 944, JFR 1558).

B. commutatus Schrad.—Infrequent along roadsides of the valley (JFR).

B. inermia Leyss.—Common under aspen near Snake River, Wildlife Range (JFR 1245).

B. japonicus Thunb.—Infrequent along roadsides of the Wildlife Range (JFR 3017).

B. tectorum L.—Common in disturbed areas (JFR 2150).
Calamagrostis canadensis (Michx.) Beauv.—Common in meadows of the Wildlife Range (JFR 2660).
C. inexpansa A. Gray.—Frequent in damp areas in Wildlife Range (JFR 1608).
Cinna latifolia (Trev.) Griseb.—Cascade Canyon trail, 8,000 ft. (JFR & Beetle 3006).
Dactylis glomerata L.—Frequent on the banks of the Snake River near Moose (RJS 946).
Danthonia californica Boland.—Dry ledges in Cascade Canyon, 7500 ft. (JFR 2994).
D. intermedia Vasey.—Frequent in elk pasture of the Wildlife Range (JFR 2508).
D. unispicata Munro.—Infrequent in sagebrush at the Square "G" Ranch (RJS 956).
Deschampsia caespitosa (L.) Beauv.—Frequent on Moose Island in the Snake River, Wildlife Range (JFR 1180).
Elymus cinereus Scribn. Merr.—Common in waste places (JFR).
E. glaucus Buckl.—Frequent along the Snake River in the vicinity of Moose (RJS 947).
Festuca idahoensis Elmer.—Common in sagebrush flats of the valley (JFR 1424).
Glyceria borealis (Nash.) Batch.—Frequent on margins of small ponds in the Wildlife Range (JFR 1500).
G. elata (Nash.) Hitchc.—Frequent in wet areas of the Wildlife Range (JFR 1566).
G. pauciflora Presl.—Frequent on margin of Pacific Creek bed (JFR 919).
G. striata (Lam.) Hitchc.—Frequent in Pacific Creek bed (JFR 917).
Hierochloe odorata (L.) Beauv.—Infrequent in the Pacific Creek area and Wildlife Range (JFR 2254).
Hordeum brachyantherum Nevski.—Common in the driest parts of willow sedge area in the Wildlife Range (JFR 1535).
H. jubatum L.—Common in waste places (JFR 1504).
Koeleria cristata (L.) Pers.—Common in the sagebrush flats (RJS 960, JFR 1410).
Melica spectabilis Scribn.—Frequent in meadows of the Wildlife Range, and on the moraines of the valley floor (RJS 907, JFR 1343).
Muhlenbergia andina (Nutt.) Hitchc.—Common in sandy area near Pacific Creek (JFR 2536).
M. filiformis (Thurb.) Rydb.—Frequent on sand in streambeds of the Wildlife Range (JFR 1577).
M. racemosa (Michx.) B.S.P.—Frequent in the meadows of the Wildlife Range (JFR 1004).
M. richardsonis Rydb.—Frequent in the pothole area south of Jackson Lake (JFR 2722).
Phalaris arundinacea L.—Infrequent in wet areas of the Wildlife Range (JFR 2761).
Phleum alpinum L.—Frequent in the major canyons from 7000 ft. to 9000 ft. (RJS).
P. pratense L.—Frequent along the Snake River from Moran south (RJS, 943, JFR 918).
Poa annua L.—Frequent in the Wildlife Range (JFR 1060).
P. canbyi (Scribn.) Piper.—Common in aspen groves and meadows of the Wildlife Range (JFR 1342).
P. fendleriana (Steud.) Vasey.—Frequent in the Elk Ranch (JFR 2321).
P. interior Rydb.—Frequent in the sagebrush flats (JFR 1407).
P. leptocoma Trin.—Frequent in wet areas of the Wildlife Range (JFR 1064).
P. nervosa (Hook.) Vasey.—Common in the forests of the Wildlife Range (JFR 2249).
P. palustris L.—Frequent in the meadows of the Wildlife Range (JFR 1393).
P. pratensis L.—Common throughout the valley floor (JFR 956).
Sitanion hystrix (Nutt.) J. G. Smith.—Frequent in waste places (JFR 1420).
Sphenopholis obtusata (Michx.) Scribn.—Infrequent along the Snake River (JFR).
Stipa columbiana Macoun.—Common in the meadows and forests of the Wildlife Range (JFR 939).
S. comata Trin. & Rupr.—Common in the sagebrush flats (JFR 1392).
S. lettermani Vasey.—Common in the sagebrush flats (JFR 1402).
S. richardsoni Link.—Frequent in the lodgepole pine forest of the Wildlife Range (JFR 947).
Trisetum spicatum (L.) Richt.—Common in the coniferous forests of the valley (JFR 1048).
T. wolfii Vasey.—Infrequent in the sagebrush of the Wildlife Range (JFR 1087).

CYPERACEAE

Carex ablata Bailey.—Cascade Canyon (FWP 11981).

C. aquatilis Wahl.—Common in the sedge meadow around Moran (JFR 997).
C. arthrostachya Olney.—Common in the meadows around Moran (JFR 5046).
C. aurea Nutt.—Common in the Wildlife Range (JFR 2274).
C. canescens L.—Cascade Canyon in wet location (FWP 11982).
C. chimaphila Holm.—Common along streambeds in Wildlife Range (JFR 995).
C. douglasii Boott.—Common in waste places of the Wildlife Range (JFR 2264).
C. eastwoodiana Stacey.—Common in the big sagebrush of the Wildlife Range (JFR 1442).
C. festivella Mack.—Common in area of Wildlife Range (JFR 991).
C. geyeri Boott.—Common in the coniferous forest of the Wildlife Range (JFR 1919).
C. gravida Bailey.—Common in the meadows of the Wildlife Range (JFR 1467).
C. hoodii Boott.—Cascade Canyon (FWP 11986).
C. interior Bailey.—Frequent in the meadows of the Wildlife Range (JFR 2247).
C. kelloggii Boott.—Cascade Canyon in wet location (FWP 11983).
C. laeviculmis Meinsh.—Cascade Canyon in wet location (FWP 11985).
C. lanuginosa Michx.—Frequent in wet areas of the Wildlife Range (JFR 1616).
C. nebraskensis Dewey.—Common in wet areas of the Wildlife Range (JFR 2322).
C. nigricans Meyer.—Shores of Amphitheater Lake (FWP 11988).
C. occidentalis Bailey.—Frequent in wet areas of the Wildlife Range (JFR 1628).
C. phaeocephala Piper.—Frequent in the meadows of the Wildlife Range (JFR 1571).
C. podocarpa R. Br.—Paintbrush Canyon in rather wet locations (FWP 11992).
C. rossii Boott.—Abundant on trail below Surprise Lake (FWP 11989).
C. rostrata Stokes.—Common in wet areas of the Wildlife Range (JFR 1499).
C. vesicaria L.—Frequent in wet areas of the Wildlife Range (JFR 1191).
Eleocharis acicularis (L.) R. & S.—Common on mud near Two Ocean Lake (JFR 2652).
E. macrostachya Britt.—Common in wet areas of the Wildlife Range, also on the shores of String Lake (RJS 958, JFR 2058).
E. obtusa (Willd.) Schultes.—Frequent in the meadows of the Wildlife Range (JFR 1981).
E. pauciflora (Lightf.) Link.—Frequent in wet areas of the Wildlife Range (JFR 1967).
Scirpus subterminalis Torr.—Rare in beaver ponds of the Moran area (JFR 1583).

LEMNACEAE

Lemna minor L.—Locally common in small quiet ponds in the vicinity of Jackson Lake Dam (RJS 911).
L. trisulca L.—Infrequent on surfaces of quiet ponds in vicinity of Jackson Lake Dam (JFR).

JUNCACEAE

Juncus balticus Willd.—Locally common in wet areas of the Wildlife Range (JFR).
J. brunnescens Rydb.—"Cascade Canyon. Plants not abundant in moist or semi-wet locations" (FWP 11930).
J. bufonius L.—Common on moist sand in the Wildlife Range (JFR).
J. confusus Coville.—Frequent in the sedge meadow of the Wildlife Range (JFR).
J. drummondii Meyer.—Hillside above Lake Solitude, 9040 ft. (LW 1709).
J. ensifolius Wikst.—Common in wet areas of the Wildlife Range (JFR).
J. filiformis L.—Rare in the sedge meadow of the Wildlife Range (JFR).
J. longistylis Torr.—Common in wet areas of the Wildlife Range (JFR).
J. mertensianus Bong.—Stream bank near Lake Solitude (LW 1702).
J. parryi Engelm.—Frequent in the sedgegrass meadows of the Wildlife Range and up to 7500 ft. on the slopes of Symmetry Spire (RJS 968).
J. saximontanus A. Nels.—Frequent along streambeds of the Wildlife Range (JFR).
J. tracyi Rydb.—Frequent in main couloir on the east face of Symmetry Spire, 8000 ft. (RJS 967).
Luzula glabrata (Hoppe) Desf.—Paintbrush Canyon (FWP 11945).

LILIACEAE

Allium brevistylum Wats.—Frequent along Snake River bottom in timber (RJS 535, LW 1211).
A. schoenoprasum L.—Infrequent in Cascade Canyon and on the slopes of Symmetry Spire up to 8500 ft. (RJS 972, LW 1227).

Brodiaea grandiflora (Lindl.) Peck.—Infrequent in the area of the Sawmill Ponds (RJS 510, LW 789).
Calochortus nuttallii Torr.—Infrequent on east side of valley on Gros Ventre Slide Road, also reported on Blacktail Butte (RJS).
Camassia quamash (Pursh.) Greene.—Locally frequent in wet meadows of the valley north of Jackson Lake Dam (RJS 518 and 841).
Disporum trachycarpum (S. Wats.) B. & H.—Frequent along the Snake River, and in the mouth of Death Canyon (RJS 739 and 1005).
Erythronium grandiflorum Pursh.—Common in North Fork of Cascade Canyon above 8000 ft. (RJS).
Fritillaria atropurpurea Nutt.—Infrequent on trails around valley lakes (RJS 622).
F. pudica (Pursh.) Spreng.—Common in the sagebrush flats (LW 1097).
Lloydia serotina (L.) Reichb.—Infrequent at the head of Death Canyon, 9600 ft. (HEB 207).
Smilacina racemosa (L.) Desf.—Frequent around the shores of the valley lakes and along the Snake River (LW 1120).
S. stellata (L.) Desf.—Frequent around the shores of the valley lakes and along the Snake River (RJS 619).
Streptopus amplexifolius (L.) DC.—Frequent along stream, trail west shore of Jenny Lake, 6794 ft. (RJS 882, LW 1221).
Tofieldia glutinosa (Michx.) Pers.—Frequent in the higher canyons and around the shores of lakes above 9000 ft. (RJS 681, LW 1195).
Veratrum californicum Dur.—Locally frequent in wet meadow beside trail to Phelps Lake, ¾ of a mile above White Grass Patrol Cabin, 6700 ft. (RJS 869).
Xerophyllum tenax (Pursh.) Nutt.—Locally frequent in wet soil at the east end of Grassy Lake Dam near divide of Reclamation Road, 10 miles west of Flag Ranch, 6900 ft. (RJS 850).
Zigadenus paniculatus (Nutt.) Wats.—Frequent in the sagebrush flats (RJS 511).
Z. venenosus S. Wats.—Locally frequent six miles up Indian Paintbrush Canyon, 9000 ft. (RJS 678).

IRIDACEAE

Sisyrinchium angustifolium Mill.—Frequent two miles north of Moose on east bank of Snake River (RJS 537).

ORCHIDACEAE

Calypso bulbosa (L.) Oakes.—Infrequent in deep shade behind Park Hdqts. and on Hidden Falls Trail (RJS 698 and 616).
Corallorrhiza maculata Raf.—Frequent in morainal soil around the shores of the valley lakes (RJS 922).
C. striata Lindl.—Rare on first switchback in the mouth of Death Canyon, 6700 ft. (RJS 843).
Goodyera oblongifolia Raf.—Rare at south end of String Lake on the String Lake Trail, also a small patch by boulder on second switchback above Hidden Falls' bridge (RJS 689 and 961).
Habenaria dilatata (Pursh.) Hook.—Infrequent in wet areas in the major canyons up to 8500 ft. (RJS 995).
H. unalascensis (Spreng.) S. Wats.—Infrequent at south boat landing on Jackson Lake (RJS 660).
Listera convallarioides (Sw.) Nutt.—Rare on west shore of Jenny Lake (RJS 542).
Spiranthes romanzoffiana Cham.—Frequent on the Snake River bottom (RJS 672).

SALICACEAE

Populus angustifolia James.—Common along the Snake River (JFR).
P. balsamifera L.—Frequent along Snake River, Wildlife Range (JFR).
P. tremuloides Michx.—Abundant in the moist habitats of the valley (RJS).
P. trichocarpa T. G.—Frequent three miles up Cascade Canyon, 8000 ft. (RJS 650).
Salix arctica Pallas.—Frequent on the shores of alpine lakes above 9000 ft. (RJS 993, LW 1708).
S. bebbiana Sarg. var. *perrostrata* (Rydb.) Schn.—Moose Post Office area (HEB).
S. brachycarpa Nutt.—Head of Granite Canyon, 9000 ft. (HEB).

S. cascadensis Ckll.—Frequent on north slope above Amphitheater Lake, 11,000 ft. (LW 1352).
S. caudata (Nutt.) Heller.—Frequent along the Snake River (JFR).
S. dodgeana Rydb.—Indian Paintbrush pass above 9500 ft. (HEB).
S. drummondiana Barr. var. *subcoerulea* (Piper) Ball.—Common along the Snake River (JFR and HEB).
S. geyeriana Anders.—Abundant along the Snake River (LW 1104).
S. lutea Nutt.—Infrequent in the Wildlife Range (JFR).
S. mackenziana (Hook.) Barr.—Infrequent in the Wildlife Range (JFR).
S. melanopsis Nutt.—Frequent in the Wildlife Range (JFR).
S. pseudocordata (Anders.) Rydb.—Common in the Wildlife Range (JFR).
S. scouleriana Barr.—Frequent in the Wildlife Range (JFR).
S. tweedyi Ball.—Head of the Death Canyon, 9000 ft. (HEB).
S. wolfii Bebb.—Frequent in the Wildlife Range (JFR).

BETULACEAE

Alnus tenuifolia Nutt.—Frequent around shores of the valley lakes and along the Snake River (RJS 621).
Betula glandulosa Michx.—Infrequent in meadow in south fork of Death Canyon (RJS 737).

MORACEAE

Humulus americanus Nutt.—Common in waste places (JFR).

URTICACEAE

Urtica gracilis Ait.—Abundant along roadsides and other waste places, especially on the Wilson Road just one mile south of Moose (RJS).

LORANTHACEAE

Arceuthobium americanum Nutt.—Frequent parasite on lodgepole pine, Jenny and String Lakes (RJS 881).

SANTALACEAE

Comandra umbellata (L.) Nutt.—Common in big sagebrush at such places as Windy Point, Timbered Island and Moose (RJS 826).

POLYGONACEAE

Eriogonum subalpinum Greene.—Frequent on the slopes of Forellen Peak 9000 ft. (RJS & R. Krear 1009).
E. umbellatum Torr.—Common in the sagebrush throughout the valley (RJS 858).
Oxyria digyna (L.) Hill.—Frequent in talus slopes of the major canyons from 7000 to 9500 ft. (LW 910).
Polygonum amphibium L.—Locally common in ponds north of Moran (RJS 654).
P. aviculare L.—Common in waste places (JFR).
P. bistortoides Pursh.—Common in the meadows north of Moran and frequent in the canyons above 9000 ft. (RJS 515).
P. buxiforme Small.—Common in waste places (JFR).
P. douglasii Greene.—Abundant throughout the valley (RJS 957).
P. fluitans Eaton.—Infrequent in wet areas of the Wildlife Range (JFR).
P. minimum S. Wats.—Infrequent in rocks on slopes of Symmetry Spire, 7200 ft. (RJS 963, LW 1402).
Rumex acetosella L.—Common in waste places throughout the valley (HEB 142).
R. crispus L.—Frequent in waste places (JFR).
R. maritimus L. var. *fueginus* (Phil.) Dusen.—Infrequent in wet places of the Wildlife Range (JFR).
R. maritima L. var. *athrix* St. John.—Infrequent on the shore of Two Ocean Lake (LW 1648).
R. mexicanus Meisn.—Frequent in open areas around Park Hdqts. (RJS 691).
R. paucifolius Nutt.—Common in the Wildlife Range (JFR).
R. triangulivalvis (Danser) Rech.—Infrequent in streambeds of the Wildlife Range (JFR).

CHENOPODIACEAE

Chenopodium capitatum (L.) Asch.—Locally common in waste places (JFR).
C. album L.—Locally common in waste places (JFR).
C. aridum A. Nels.—Common in waste places of the valley (JFR).
Kochia scoparia Schrad.—Common in waste places of the valley (JFR).
Monolepis nuttalliana (R. & S.) Engelm.—Common in waste places of the valley (JFR).
Salsola kali L.—Common in waste places of the valley (JFR).

PORTULACACEAE

Claytonia lanceolata Pursh.—Common in the valley in the big sagebrush and lodgepole pine communities, also in higher canyons such as the North and South Forks of Cascade Canyon (RJS).
Lewisia minima A. Nels.—Rare in sagebrush flats east of Jenny Lake south checking station ¼ mile (RJS).
L. pygmaea (Gray) Robins.—Head of Death Canyon, 9600 ft. (HEB 221).
L. triphylla (S. Wats.) Robins.—Infrequent in wet moss ¼ mile below Hidden Falls (RJS 646 and 909).

CARYOPHYLLACEAE

Arenaria congesta Nutt.—Abundant in the sagebrush flats and moraines of the valley (RJS).
A. lateriflora L.—Infrequent in aspen groves of the Wildlife Range (JFR).
A. nuttallii Pax.—Rare on very top of divide between South Cascade and Alaska Basin, 10,000 ft. (RJS 1012).
Cerastium arvense L.—Frequent near Sawmill Ponds on the Wilson Road, also Snake River bottom (LW 1116).
Sagina saginoides (L.) Britt.—Common in streambeds and waste places in Pacific Creek area (LW 1734).
Silene acaulis L.—Frequent in rocks around alpine lakes, up to 10,000 ft. (RJS 679).
S. menziesii Hook. —Infrequent in the area of Cow Lake, southeast of Signal Mountain (RJS 645).
S. noctiflora L.—Rare, horse concession on Cottonwood Creek (RJS 692).
S. parryi (S. Wats.) H. & M.—Frequent at the head of Death Canyon (RJS 687).
Spergularia rubra (L.) Presl.—Common in the open areas of the sagebrush flats (JFR and RJS).
Stellaria longifolia Muhl.—Frequent in the shrub-swamp of the Wildlife Range (JFR).
S. longipes Goldie.—Common in the meadows of the Wildlife Range (JFR).

NYMPHAEACEAE

Nuphar polysepalum Engelm.—Common in beaver ponds of the valley (RJS 655).

CERATOPHYLLACEAE

Ceratophyllum demersum L.—Frequent near the outlet of Two Ocean Lake (RJS 710½).

RANUNCULACEAE

Aconitum columbianum Nutt.—Locally common in wet areas and along streams in the valley and extending into the major canyons up to 9000 ft. (RJS).
Actaea arguta Nutt.—Frequent in the major canyons and around the shores of the valley lakes (RJS 695).
Anemone cylindrica Gray.—Frequent ½ mile below Moose on the west bank of the Snake River (RJS 856).
A. globosa Nutt.—Infrequent below moraine of School Room Glacier, South Cascade Canyon, 9500 ft. (RJS & R. Krear 927, HEB 225).
Aquilegia caerulea James.—Common in the major canyons up to 9000 ft. (LW 1672).
Caltha leptosepala DC.—Frequent in alpine meadows above 8500 ft. (RJS 651).
Clematis columbiana (Nutt.) T. & G.—Infrequent on Beaver Creek Trail ¼ mile west Pk. Hdqts. (RJS 848).
C. hirsutissima Pursh.—Infrequent at the base of Black-tail Butte, also in some of the higher canyons above 9000 ft. (RJS 615 & 928).

C. ligusticifolia Nutt.—Infrequent on trail, two miles up Death Canyon, 7500 ft. (RJS 755).

Delphinium nelsoni Greene.—Common in gravelly soil throughout the valley (RJS 835).

D. occidentale (Wats.) Wats.—Frequent along second Saw Mill Pond, 1¼ mile southwest from Moose (RJS 857).

Myosurus minimus L.—Across the Snake River from University of Wyoming. Biological Station (WGS 3889).

Paeonia brownii Dougl.—Locally frequent between road and the lake in front of the Jenny Lake Museum (RJS 617).

Ranunculus acriformis Gray. var. *montanensis* (Rydb.) L. Benson.—Frequent in wet places, north and east of Moran (RJS 634).

R. aquatilis L. var. *capillaceus* (Thuill.) DC.—Frequent in pools and sluggish streams throughout the valley (RJS and JFR).

R. cymbalaria (Pursh.) Greene—Common in wet places of the Wildlife Range (JFR).

R. eschscholtzii Schlect.—Infrequent on the east shore of Lake Solitude, 9024 ft. (RJS 952, LW 922).

R. glaberrimus Hook.—Frequent in the Wildlife Range (JFR).

R. inamoenus Greene.—Frequent in sedge meadow of Wildlife Range, also Park Hdqts. (RJS 624).

R. natans C. A. Meyer.—Common in wet places of the Wildlife Range (JFR).

R. sceleratus L. var. *multifidus* Nutt.—Common in wet places of the Wildlife Range (JFR).

R. jovis A. Nels.—Abundant in the early spring on the sagebrush flats throughout the valley floor (RJS 905).

Thalictrum fendleri Engelm.—Frequent in the coniferous forest on the moraines of the valley (RJS 626).

T. occidentale Gray.—Frequent in wet areas of the Wildlife Range (JFR).

T. sparsiflorum Turcz.—Infrequent on the west shore of Jenny Lake (RJS 644).

Trollius laxus Salisb.—Frequent in wet meadow one mile below Lake Solitude, 8600 ft. (RJS 652 and 930).

BERBERIDACEAE

Mahonia repens (Lindl.) G. Don.—Frequent around the shores of the valley lakes (LW 1692).

FUMARIACEAE

Dicentra uniflora Kellogg.—Infrequent in the areas of Park Hdqts. and the Jenny Lake Museum (RJS).

Corydalis aurea Willd.—Locally frequent along Snake River, south of Signal Mountain (RJS and C. Jepson 859).

CRUCIFERAE

Arabis drummondii A. Gray.—Frequent in the sagebrush of the Wildlife Range (JFR 2134).

A. exilis A. Nels.—Common in the waste places of the Wildlife Range (JFR 1643).

A. glabra (L.) Bernh.—Frequent in the Wildlife Range (JFR 1324).

A. hirsuta Scop.—Frequent in the meadows of the Wildlife Range (JFR 2137).

A. holboellii Hornem.—Common on the moraines and sagebrush flats (RJS 502, JFR 2176).

A. nuttallii Robinson.—Frequent in the meadows of the Wildlife Range (JFR 1998).

Barbarea americana Rydb.—Infrequent in the Wildlife Range (JFR 2318).

Capsella bursa-pastoris (L.) Medic.—Common in waste places throughout the park.

Cardamine breweri Wats.—Frequent in the Wildlife Range (JFR 2862).

Descurainia pinnata (Walt.) Britt.—Frequent in waste places throughout the park.

D. sophia (L.) Webb.—Frequent in waste places (JFR 1658).

Draba stenoloba Ledeb. var. *nana* (Schulz.) Hitchc.—Common in the Wildlife Range (JFR 1836).

Erysimum cheiranthoides L.—Infrequent in aspen groves of the Wildlife Range (JFR).

E. wheeleri Rothr.—Infrequent on Cascade Canyon switchbacks above Hidden Falls Bridge, 6800 ft. (RJS 845 and 641).

Lepidium campestre (L.) R. Br.—Common in waste places (JFR 1281).

L. densiflorum Schrad. var. *bourgeauanum* (Thell.) Hitchc.—Common in the sagebrush flats of the valley (JFR 2516).
L. perfoliatum L.—Frequent in waste places (JFR 2754).
Lesquerella prostrata A. Nelson.—Rare on sandy areas of the Wildlife Range (JFR 1807).
Physaria australis (Pays.) Rollins.—Infrequent on switchbacks just north of the Schoolroom Glacier, South Cascade Canyon, 10,000 ft. (RJS 1011).
Rorippa curvisiliqua (Hook.) Bess.—Frequent around edge of pond just north of Square "G" Ranch (RJS 918)
R. palustris (L.) Bess.—Common in wet areas of the Wildlife Range (JFR 2523).
R. nasturtium-aquaticum (L.) Schenz. & Thell.—Frequent on delta at the mouth of Cascade Creek west shore of Jenny Lake (RJS 885).
Smelowskia calycina (Stephan) Mey.—Frequent on switchbacks beside the Schoolroom Glacier, 10,000 ft., South Cascade Canyon (RJS 711).
Thlaspi arvense L.—Common in waste places (RJS 637).
T. parviflorum A. Nels.—Common in the meadows of the Wildlife Range (JFR 1990).

CRASSULACEAE

Sedum debile Wats.—Frequent on rocky bank near Bradley Lake and Cascade Canyon (LW 1396 and 1689).
S. rhodanthum Gray.—Rare on trail in Indian Paintbrush Canyon, two miles below Holly Lake turnoff, 8800 ft. (RJS 977 and 989).
S. stenopetalum Pursh.—Common in sagebrush flats (RJS 1014, JFR 2158).

SAXIFRAGACEAE

Heuchera parvifolia Nutt. var. *utahensis* (Rydb.) Garrett.—Infrequent on trail, Phelps Lake Lookout, also Blacktail Butte (RJS 673, LW 1757).
Lithophragma bulbifera Rydb.—Frequent in the sagebrush flats of the valley (RJS 906).
L. parviflora (Hook.) Nutt.—Frequent in wet meadow near Two Ocean Lake (RJS 636).
Mitella pentandra Hook.—Frequent along stream in the major canyons (RJS 934).
M. stauropetala Piper.—Rare on trail to Hidden Falls (RJS 846).
M. stenopetala Piper.—Frequent on major trails in canyons also Glacier Trail, below 8500 ft. (RJS 640 and 846).
Parnassia fimbriata Koenig.—Frequent around the shore of Jenny Lake and along banks of streams in the canyons (RJS 685).
P. parviflora DC.—Frequent in wet areas around Moran and the banks of the Snake River (RJS 674).
Ribes aureum Pursh.—Reported by HEB.
R. montigenum McCl.—Head of Death Canyon, also Granite and Waterfall Canyons (HEB).
R. petiolare Dougl.—Frequent in the mouths of Death and Cascade Canyons (RJS 938).
Saxifraga bronchialis L.—Locally common on boulders in Hidden Falls area, also above Laurel Lake (RJS 552 and 936).
S. punctata L. var. *arguta* (D. Don.) Engl. & Irmsch.—Frequent along streams of the major canyons (RJS 683 and 933).
S. oppositifolia L.—Rare in rock crevices, deep shade, north facing slope on trail to Teton Glacier just before hand cable, 10,000 ft. (RJS 851).
S. rhomboidea Greene.—Frequent on wet mossy area, mouth of Cascade Canyon (RJS 910, LW 1135).
Telesonix jamesii (Torr.) Raf. *heucheriformi* (Rydb.) Bacigalupi.—Frequent in rocks last switchback, six miles up Indian Paintbrush Canyon, 8500 ft. (RJS 677, LW 914).

ROSACEAE

Amelanchier alnifolia Nutt.—Common along the Snake River and around the shores of the valley lakes (RJS).
Cercocarpus ledifolius Nutt.—Infrequent in the lower portions of Granite Canyon (HEB 15).
Crataegus douglasi Lindl.—Frequent along Snake River (LW 1213).
Dryas octopetala L.—Cliff above Indian Lake, Granite Canyon. Infrequent in rocky soil above 9500 ft., Schoolroom Glacier, Cascade Canyon (RJS 726 & 1015).
Fragaria bracteata Heller.—Frequent on the moraines of the valley floor (RJS 614).

F. glauca (S. Wats.) Rydb.—Common in sagebrush of the Wildlife Range (JFR 2044).
Geum macrophyllum Willd.—Frequent in the meadows of the Wildlife Range, also Double Diamond Ranch (JFR 1152, LW 1219).
G. rossii (R. Br.) Ser.—Frequent on Avalanche Canyon Divide, 10,000 ft., (RJS 760).
G. triflorum Pursh. var. *ciliatum* (Pursh.) Fassett.—Frequent in meadows and sagebrush flats of the valley (RJS 504, JFR 1876).
Ivesia gordonii (Hook.) T. ex G.—Infrequent on divide of Upper Death Canyon, also Main Highway 4 miles north of Moran (RJS 758 and 516).
Potentilla anserina L.—Frequent on mud flats of Jackson Lake one mile above Lizard Point (RJS 1006).
P. arguta Pursh. ssp. *typica* Keck.—Frequent in meadows of the Wildlife Range (JFR 1313).
P. arguta Pursh. ssp. *convallaria* (Rydb.) Keck.—Frequent in the meadows of the Wildlife Range (JFR 1031).
P. diversifolia Lehm.—Common in the meadows of the Wildlife Range (JFR 1996).
P. fruticosa L.—Common along Snake River and frequent in the canyons (RJS 517).
P. glandulosa Lindl. ssp. *glabrata* (Rydb.) Keck.—Frequent in meadows on road to Two Ocean Lake (RJS 632).
P. gracilis Dougl. ssp. *nuttallii* (Lehm.) Keck.—Common in the meadows of the Wildlife Range (JFR 1260).
P. monspeliensis L.—Infrequent on bank of Snake River east of Moran (JFR 2524).
P. pectinisecta Rydb.—Frequent in meadows north of Park Hdqts. (RJS 625).
Prunus virginiana L. var. *melanocarpa* (Nels.) Sarg.—Common along Snake River and on the moraines of the valley (JFR 2209).
Purshia tridentata (Pursh.) DC.—Common in the sagebrush flats of the valley (RJS 509).
Rosa woodsii Lindl.—Common along the banks of the Snake River (JFR 2537).
Rubus parviflorus Nutt.—Common on the moraines and abundant in the lower portions of the major canyons (JFR 2553).
R. strigosus Michx.—Infrequent along Snake River east of Moran, also frequent in talus slopes of the major canyons (RJS 996, JFR 2521).
Sibbaldia procumbens L.—Frequent on shores of alpine lakes above 9000 ft. (RJS 715).
Sorbus scopulina Greene.—Common on the lower slopes of the mountains and along the shores of the valley lakes (RJS. JFR 2860).
Spiraea densiflora Nutt.—Frequent on mountain slopes and in the major canyons up to 9000 ft. (RJS).
S. lucida Dougl.—Frequent on the moraines and shores of the valley lakes (RJS).

LEGUMINOSAE

Astragalus agrestis Dougl.—Frequent in the sedgegrass meadow of the Wildlife Range (JFR).
A. alpinus L.—Common in the Wildlife Range (JFR).
A. bisulcatus (Hook.) A. Gray.—Infrequent, east park boundary (RJS 526).
A. bodini Sheld.—Infrequent in the Wildlife Range (JFR).
A. canadensis L.—Sandy river bottom, near Bar. BC Ranch (LW 1342).
A. decumbens (Nutt.) Gray.—Infrequent near outlet of Two Ocean Lake (RJS 631).
A. glareosus Dougl.—Frequent in the Wildlife Range (JFR).
A. tegetarius S. Wats.—Rare in rocks on Surprise Lake Lookout, 10,000 ft. (RJS 855).
A. terminalis Wats.—Common on the dry terraces above the Snake River (RJS 915).
Caragana arborescens Lam.—Remaining from cultivation in the Wildlife Range (JFR).
Glycyrrhiza lepidota (Nutt.) Pursh.—Common along the Snake River bottoms (LW 1340).
Hedysarum boreale Nutt.—Frequent on trail at the head of So. Cascade Canyon and on the slopes of Symmetry Spire (RJS 750 and 970).
Lupinus argenteus Pursh.—Common on the east shore of Jackson Lake (RJS 981).
L. polyphyllus Lindl.—Frequent on dry rocky flats of the valley (LW 1117).
L. sericeus Pursh.—Abundant throughout the valley (RJS, 656, LW 1621).
Medicago lupulina L.—Common in waste places throughout the valley (JFR).
M. sativa L.—Common in waste places of the Wildlife Range (JFR).
Melilotus alba Desv.—Common along the highways and waste places (RJS).

M. officinalis (L.) Lam.—Common along the highways and waste places (RJS 945).
Oxytropis deflexa (Pall.) DC.—Frequent along the Snake River (LW 1341 and 1646).
Trifolium hybridum L.—Common in waste places of the Wildlife Range (JFR).
T. pratense L.—Common in waste places of the Wildlife Range (JFR).
T. repens L.—Frequent in waste places of the valley (HEB 186).
T. rydbergii Greene.—Common in meadows of the Wildlife Park (JFR).
Vicia americana Muhl.—Frequent along the Snake River (RJS 916).

GERANIACEAE

Geranium nervosum Rydb.—Common along Snake River and open xeric sites of the moraines (RJS 643).
G. richardsonii Fisch. & Trautv.—Frequent on stream banks or moist areas such as behind Park Hdqts., String Lake, and road to Two Ocean Lake (RJS 556).

LINACEAE

Linum lewisii Pursh.—Frequent in the area of the Wildlife Range (RJS 710).

CALLITRICHACEAE

Callitriche palustris L.—Common in pools and adjacent mud of the Wildlife Range (JFR).

LIMNANTHACEAE

Floerkea proserpinacoides Willd.—Infrequent in the Wildlife Range (JFR).

CELASTRACEAE

Pachystima myrsinites Raf.—Common on moraines and shores of the valley lakes (RJS).

ACERACEAE

Acer glabrum Torr.—Infrequent on west shore of Jenny Lake, also on slopes between Laurel and String Lakes (LW 1344).

RHAMNACEAE

Ceanothus velutinus Dougl.—Frequent around the shores of the valley lakes (LW 1207).
Rhamnus alnifolia L'Her.—Frequent in the Sawmill Ponds area and on the shore of Jackson Lake (JFR, HEB).

MALVACEAE

Sphaeralcea rivularis (Dougl.) Torr.—Common along roadsides and waste places (RJS 978).

HYPERICACEAE

Hypericum formosum H.B.K.—Frequent in the major canyons above 8000 ft. (RJS 666).

VIOLACEAE

Viola adunca J. E. Smith.—Frequent on the north and east shores of Lake Solitude, 9024 ft., also on the west bank of the Snake River (RJS 953 & 914).
V. macloskeyi Lloyd.—Infrequent at the base of Hidden Falls (RJS 937).
V. praemorsa Doug. ssp. *linguaefolia* (Nutt.) Baker & Clausen.—Frequent in moist places in the timber, throughout the valley (RJS 611, LW 1091).
V. purpurea Kell. var. *venosa* Brainerd.—Frequent on the east shore of Jenny Lake (RJS 618).

LOASACEAE

Mentzelia laevicaulis (Dougl.) T. & G.—Frequent on dry hillside above Highway 89, 7 miles south of Jackson (RJS 751, also reported in Moran area by C. Jepson).

CACTACEAE

Opuntia fragilis (Nutt.) Haw.—Frequent on banks of Snake River in area of Deadman's Bar (RJS 880).

ELAEAGNACEAE

Elaeagnus commutata Bernh.—Frequent along the Snake River (RJS 849).
Shepherdia canadensis (L.) Nutt.—Common along the banks of the Snake River and shores of the valley lakes (RJS 985).

ONAGRACEAE

Epilobium adenocaulon Hausskn.—Common in wet places of the Wildlife Range (JFR).
E. alpinum L.—Frequent in couloirs and canyons above 8000 ft. (RJS 975).
E. angustifolium L.—Abundant along roadsides throughout the valley (RJS).
E. latifolium L.—Frequent by streams in Garnet Canyon and the upper part of South Cascade Canyon, 9500 ft. (RJS 741).
E. paniculatum Nutt.—Abundant in sagebrush, Blacktail Butte, 6600 ft. (RJS 917).
E. suffruticosum Nutt.—Frequent in gravel of the Snake River bottom (LW 1338 and 1637).
Gayophytum diffusum T. & G. Frequent in disturbed areas throughout the valley (RJS).
Oenothera heterantha Nutt.—Frequent in the meadows north and east of Moran (RJS 913).
O. hookeri T. & G.—Common along main highway between Jenny Lake and south boundary (RJS 540).
O. pallida Lindl.—Infrequent on trail to fire lookout on Black-tail Butte (RJS 693).
Zauschneria garrettii A. Nels.—Frequent on rocky ledges in such canyons as Death, Waterfall, and Cascade, up to 7500 ft. (RJS 680 and 994).

HALORAGIDACEAE

Hippurus vulgaris L.—Infrequent in ponds and pools north of the town of Moran (RJS 657 and 921).
Myriophyllum exalbescens Fern.—Swan Lake (WGS 3998).

UMBELLIFERAE

Angelica pinnata S. Wats.—Common on the forested moraines of the valley (RJS 642).
Heracleum lanatum Michx.—Common in moist areas throughout the valley and lower parts of the canyons (RJS).
Ligusticum filicinum Wats.—Frequent in moist aspen groves and coniferous forests of the valley and major canyons (RJS 1007, HEB 278).
Lomatium simplex (Nutt.) Macbr.—Frequent in the Wildlife Range (JFR).
Osmorhiza chilensis Hook. & Arn.—Frequent in deep shade back of Park Hdqts. (RJS 628).
O. obtusa (C. & R.) Fernald.—Bank of Bradley Creek, 7000 ft. (LW 1128).
O. occidentalis (Nutt.) Torr.—Common in aspen stands of the Wildlife Range (JFR).
Perideridia gairdneri (H. & A.) Mathias.—Common throughout the valley floor (RJS 690).
Pteryxia hendersoni (C. & R.) M. & C.—Frequent on the trail to the head wall of South Cascade Canyon, 9800 ft. (RJS 1013).
Sium suave Walt.—Infrequent in ponds of the Wildlife Range (JFR).

CORNACEAE

Cornus stolonifera Michx.—Frequent around the shores of the valley lakes, also at Park Hdqts. (JFR 2734).

ERICACEAE

Arctostaphylos uva-ursi (L.) Spreng.—Frequent in the area of Signal Mountain (JFR 952).
Chimaphila umbellata (L.) Nutt.—Frequent along the shores of such lakes as Leigh, String and Jenny (RJS 662).
Gaultheria humifusa (Graham) Rydb.—Infrequent on the rocky shores of Bradley Lake (LW 1030 and 1389).
Kalmia polifolia Wang.—Frequent on the shores of String, Jenny and Taggart Lakes (RJS 630).
K. polifolia Wang var. *microphylla* (Hook.) Rehd.—Frequent on the shores of alpine lakes above 9000 ft. (LW 1354).
Menziesia ferruginea Smith.—Frequent along the shores of the valley lakes (RJS 639).
Moneses uniflora (L.) Gray.—Frequent in timber at the head of Bradley Lake (LW 1388 and 1050).
Monotropa hypopitys L.—Rare in deep shade on the east shore of Leigh Lake (RJS 730).
Phyllodoce empetriformis (Sm.) D. Don.—Frequent around the shores of lakes above 9000 ft. (RJS 536 and 991).

P. glanduliflora (Hook.) Coville.—Frequent above Amphitheater Lake, 9500 ft. (LW 896 and 1355).
Pterospora andromedea Nutt.—Frequent around the shores of the valley lakes (RJS 729).
Pyrola asarifolia Michx.—Frequent in the coniferous forest of the valley (RJS 544).
P. secunda L.—Frequent around the shores of the valley lakes (RJS 543).
Vaccinium membranaceum Dougl.—Abundant in the canyons and around the shores of the valley lakes (RJS).
V. occidentale A. Gray.—Infrequent near the outlet of Bradley Lake (RJS 727).
V. scoparium Leiberg.—Abundant in the canyons and on the moraines of the valley (RJS).

PRIMULACEAE

Androsace septentrionalis L. var. *diffusa* Knuth.—Infrequent along stream, Park Hdqts. (RJS 699).
A. septentrionalis L. var. *subumbellata* A. Nels.—Frequent at the head of Death Canyon, also reported at the Wildlife Range (HEB 220, JFR).
Dodecatheon conjugens Greene.—Frequent, in the sagebrush flats, especially around the Jenny Lake region (RJS 610, LW 2178).
Primula parryi Gray.—Frequent in the higher canyons and on mountain slopes above 9000 ft. (RJS).

GENTIANACEAE

Gentiana affinis Griseb.—Frequent along Snake River (RJS 675).
G. amarella L.—Frequent in streambed with mosses on north side of Signal Mt. (RJS 979).
G. calycosa Griseb.—Frequent in major canyons above 8000 ft. (RJS 988 & 668).
G. thermalis O. Ktze.—Frequent along small streams in willow areas one mile north of Moran (RJS 658).
Swertia perennis L.—Frequent along stream in South Fork of Death Canyon 8500 ft. (RJS 738).
S. radiata (Kellogg) Ktze.—Common along Snake River also such places as Wildlife Range and Blacktail Butte (LW 1722).

APOCYNACEAE

Apocynum androsaemifolium L.—Frequent around the shores of the valley lakes (RJS 663, LW 1679).

POLEMONIACEAE

Collomia linearis Nutt.—Common in the sagebrush flats throughout the valley (RJS 514).
Gilia aggregata (Pursh.) Spreng.—Common in gravelly soil, usually associated with big sagebrush, throughout the valley floor (RJS 505).
Linanthus nuttallii (A. Gray) Greene.—Frequent in Death Canyon and southern peaks of the range above 7500 ft. (RJS 669).
L. septentrionalis Mason.—Infrequent, Snake River bottom (LW 1636).
Phlox caespitosa Nutt.—Infrequent on ledges above Amphitheater Lake, 9800 ft. (LW 1353).
P. longifolia Nutt. ssp. *calva* Wherry.—Frequent in the big sagebrush throughout the valley (RJS 503).
Polemonium occidentale Greene.—Frequent in wet areas in the vicinity of the Sawmill Ponds, also north of Moran (RJS 546).
P. viscosum Nutt.—Frequent at elevations above 9000 ft. (RJS 549).

HYDROPHYLLACEAE

Hydrophyllum capitatum Dougl.—Frequent on moraines in such areas as Park Hdqts., Jenny Lake Campground, and Wildlife Range (RJS 613).
Nemophila breviflora A. Gray.—Locally common along shore of Snake River at Menor's Ferry (RJS 746).
Phacelia heterophylla Pursh.—Common in waste places (RJS 923).
P. idahoensis Hends.—Frequent in the major canyons of the range (RJS 661).
P. leucophylla Torr. var. *alpina* (Rydb.) Dundas.—Frequent in rocks on the east slope of Symmetry Spire up to 8000 ft. (RJS 962).

BORAGINACEAE

Cryptantha affinis (Gray) Greene.—Common in waste places east of Moran (JFR).
Cynoglossum officinale L.—Infrequent near south checking station on Jenny Lake Road (RJS).
Eritrichium elongatum (Rydb.) Wight.—Locally frequent above 10,000 ft. on such peaks as Grand Teton, Middle Teton, and Disappointment (RJS 748 and 861).
Hackelia diffusa (Lehm.) I. M. Johnst.—Frequent in aspen groves of the Wildlife Range (JFR).
H. floribunda (Lehm.) I. M. Johnst.—Common in waste places (JFR).
H. jessicae (McGreg.) Brand.—Frequent along the Snake River (RJS 507).
H. patens (Nutt.) I. M. Johnst.—Common on roadside cuts around the town of Moose (RJS 506).
Lappula cenchroides A. Nels.—Common in waste places (JFR).
Lithospermum ruderale Dougl.—Frequent along Snake River extending out into the sagebrush flats (RJS).
Mertensia ciliata (James) G. Don.—Frequent in moist places in the major canyons up to 9000 ft. (RJS 1016).
Plagiobothrys cognatus (Greene) I. M. Johnst.—Shore of Jackson Lake (LW 1628).
P. cusickii (Greene) I. M. Johnst.—Locally common around small pond just north of the Square "G" Ranch (RJS 919).

LABIATAE

Agastache urticifolia (Benth.) Ktze.—Common on morainal soil Taggart and Bradley Lakes areas, also Glacier Trail, and Wildlife Range (RJS 513).
Dracocephalum nuttallii Britt.—Infrequent along the banks of the Snake River (HEB 65).
Mentha arvensis L.—Infrequent along the Snake River (RJS 667).
Prunella vulgaris L.—Frequent along Snake River below Moose, also along east shores of Leigh and String Lakes (RJS 539).
Scutellaria galericulata L.—Frequent in the meadows north of the Jackson Lake Dam (RJS 980).

SCROPHULARIACEAE

Besseya cinera (Raf.) Penn.—Infrequent on tableland at head of Death Canyon, 9600 ft. (HEB 192).
Castilleja longispica A. Nels.—Frequent on morainal soil throughout the valley (RJS 828).
C. rhexifolia Rydb.—Locally common in wet areas north of Moran (RJS 633).
C. linariaefolia Benth.—Infrequent in the willows of the Wildlife Range (JFR).
C. septentrionalis Lindl.—Frequent two miles up North Fork of Cascade Canyon (RJS 684).
Collinsia parviflora Dougl.—Abundant throughout valley floor, under lodgepole, aspen and sagebrush (JFR and RJS).
Linaria vulgaris Hill.—Locally common in waste places throughout the valley (RJS).
Mimulus floribundus Dougl.—Rare in Cascade Canyon and Death Canyon up to 8000 ft. (LW 1676).
M. guttatus DC.—Locally common in wet places and stream banks north of Moran on Highway 89 (RJS 638).
M. lewisii Pursh.—Locally common along streams in the higher canyons (RJS 555, LW 1346).
M. moschatus Dougl.—Infrequent in the mouths of the major canyons (LW 1189).
Orthocarpus luteus Nutt.—Common along the Snake River and in the Sagebrush flats (RJS 986, FWP 11935).
Pedicularis bracteosa Benth.—Frequent in the coniferous forest from 6700 ft., up to 9000 ft. (RJS 522).
P. contorta Benth.—Locally frequent on south facing slope above trail, ¼ mile above turn off to Holly Lake, Indian Paintbrush Canyon, 9400 ft. (RJS 874).
P. groenlandica Retz.—Abundant in the sedge meadows ½ mile north of Moran, also ½ mile below Lake Solitude (RJS 682).
P. racemosa Dougl.—Frequent on morainal soil, trails to Taggart, Bradley and Leigh Lakes, also high canyons (LW 1345).

Penstemon cyananthus Hook. ssp. *subglaber* (Gray) Penn.—Frequent in disturbed areas throughout the valley (RJS 524).
P. deustus Dougl.—Infrequent on switchbacks above Hidden Falls, Park Hdqts., mouth of Death Canyon (RJS 534).
P. ellipticus Coult. & Fischer.—Rare in rocks on switchbacks above Lake Solitude, also at 10,000 ft. in the South Fork of Cascade Canyon (RJS 723).
P. procerus Dougl.—Frequent in disturbed places throughout the valley (RJS 523).
P. radicosus A. Nels.—Infrequent on north end of Blacktail Butte (LW 1755).
P. whippleanus Gray.—Frequent on trails in such canyons as Death and Cascade Canyons (RJS 671).
Scrophularia lanceolata Pursh.—Locally frequent in the following canyons: (by trail always on rocky south facing slopes) Cascade, Garnet, Death and Indian Paintbrush (RJS 844 and 876).
Verbascum thapsus L.—Infrequent in disturbed areas around the Jackson Lake Lodge (RJS).
Veronica americana Schwein.—Frequent on mud of Wildlife Range and area below Hidden Falls (RJS 547).
V. peregrina L. var. *xalapensis* (HBK) St. John & Warren.—Frequent on the shore of Jackson Lake (LW 1625).
V. serpyllifolia L. var. *humifusa* (Dicks.) Vahl.—Frequent in sedge meadow near Swan Lake (RJS 920).
V. wormskjoldii Roem. & Schult.—Infrequent in upper portions of North and South Cascade Canyons (Cottam 12226, RJS 627).

OROBANCHACEAE

Orobanche fasciculata Nutt.—Rare as a parasite on big sagebrush throughout the valley floor (RJS 649 and 955).
O. uniflora L.—Rare in wet mossy places in the mouth of Cascade Canyon (RJS 647).

LENTIBULARIACEAE

Utricularia vulgaris L.—Rare in beaver pond ¼ mile south of Jackson Lake Dam on main highway (RJS 659).

PLANTAGINACEAE

Plantago lanceolata L.—Locally common in waste places of the valley (JFR).
P. major L.—Locally common in waste places of the valley (RJS 983).

RUBIACEAE

Galium bifolium Wats.—Frequent under the aspen at the Wildlife Range (RJS 912).
G. boreale L.—Common on the moraines of the valley (RJS).
Kelloggia galioides Torr.—Infrequent in the main couloir on the east face of Symmetry Spire, 7600 ft. (RJS 964).

CAPRIFOLIACEAE

Linnaea borealis L. var. *americana* (Forbes) Rehd.—Frequent on the slopes of Signal Mountain (RJS 722).
Lonicera involucrata Banks.—Frequent around the shores of the valley lakes (RJS 629).
L. utahensis S. Wats.—Common in the coniferous forest of the valley and canyons (RJS).
Sambucus melanocarpa Gray.—Frequent around the shores of the valley lakes and along the Snake River (JFR).
S. microbotrys Rydb.—Frequent two miles up Indian Paintbrush Canyon (RJS 987).
Symphoricarpos occidentalis Hook.—Frequent in moist aspen groves of the Wildlife Range (JFR).
S. rivularis Suksd.—Common in waste places (JFR).
S. tetonensis A. Nels.—Frequent in sagebrush flats of the valley (RJS 530).
S. vaccinioides Rydb.—Frequent in the sagebrush flats of the valley (RJS 924).

VALERIANACEAE

Valeriana obovata (Nutt.) R. & S. ssp. *obovata* Meyer.—Frequent in meadows of the Wildlife Range (JFR).
V. occidentalis Heller.—Infrequent above Phelps Lake Lookout on Skyline Trail, 9500 ft. (RJS 670).

CAMPANULACEAE

Campanula rotundifolia L.—Common along roadsides throughout the valley, also in coniferous forests (RJS 984).

Porterella carnosula (H. & A.) Torr.—Locally frequent in shallow water at the margin of the pond at the west base of Signal Mountain (RJS 870).

COMPOSITAE

Achillea lanulosa Nutt.—Abundant throughout the valley and lower portions of the major canyons (RJS).

A. lanulosa Nutt. ssp. *alpicola* (Rydb.) Keck.—Locally frequent on south facing slope above trail, ¼ mile above turn off to Holly Lake, Indian Paintbrush Canyon, 9500 ft. (RJS 877).

Actinea grandiflora (T. & G.) Kuntze.—Frequent along Skyline Trail above 9500 ft. (RJS 665).

Agoseris aurantiaca (Hook.) Greene.—Frequent up to 9000 ft., in the major canyons (RJS 976).

A. elata (Nutt.) Greene.—Frequent in irrigated field of the Elk Ranch (JFR 2329).

A. glauca (Nutt.) Greene.—Frequent along the Snake River (JFR).

A. glauca (Nutt.) Greene var. *laciniata* (Eat.) Smiley.—Frequent in the meadows of the Wildlife Range (JFR 2181).

A. purpurea (A. Gray) Greene.—Frequent on first terrace above Pacific Creek (JFR 936).

Anaphalis margaritacea (L.) Benth. & Hook.—Frequent ¼ mile above main bridge, Indian Paintbrush Canyon, 8400 ft. (RJS 878).

Antennaria aprica Greene.—Frequent in Cascade Canyon also at the Wildlife Range (LW 1225, JFR 2146).

A. arida E. Nels.—Common in the sagebrush flats near Moose (LW 1639, JFR 2169).

A. corymbosa E. Nels.—Common in the sagebrush flats west of Moose (JFR 2227).

A. dimorpha (Nutt.) T. & G.—Infrequent in sagebrush flats of the valley (JFR 1877).

A. luzuloides T. & G.—Frequent in the Snake River bottoms (JFR 2115, LW 1220).

A. parvifolia Nutt.—Common on dry terraces of the Pacific Creek area (JFR 961).

A. racemosa Hook.—Common on the north exposure of Signal Mt. (LW 40, JFR 2750).

A. rosea (Eat.) Greene.—Common in sagebrush flats and moraines of the valley (RJS 533, JFR 1021).

Arnica longifolia D. C. Eaton ssp. *genuina* Maguire.—Locally common in canyons and couloirs from 7500 ft. to 10,000 ft. (RJS 969, LW 1404).

A. chamissonis Less. ssp. *foliosa* (Nutt.) Maguire.—Locally common in moist places in timber, Snake River bottoms (LW 1332).

A. cordifolia Hook.—Common in the coniferous forests of the valley (RJS).

A. latifolia Bong.—Frequent in the major canyons, 7000 to 8000 ft. (LW 1667).

A. mollis Hook. var. *genuina* Maguire.—Frequent in bog west of Taggart Lake (LW 1191).

Artemisia abrotanum L.—Remaining from previous cultivation (JFR 2533).

A. arbuscula Nutt. Locally common on valley floor north of Park Hdqts. (RJS).

A. cana Pursh.—Locally common along the Snake River (JFR 1131).

A. dracunculoides Pursh.—Infrequent in waste places (JFR 2763).

A. ludoviciana Nutt. ssp *candicans* (Rydb.) Keck.—Frequent along the Snake River (RJS 954, JFR 3061).

A. ludoviciana Nutt. ssp. *typica* Keck.—Frequent in the drier regions of the Wildlife Range (RJS 982, JFR 1135).

A. tridentata Nutt.—Abundant throughout the valley.

A. tripartita Rydb.—Locally common in the big sagebrush of the valley (JFR 1830).

Aster alpigenus (T. & G.) Gray ssp. *haydeni* (Porter) Cron.—Frequent on the shores of alpine lakes above 9000 ft. (RJS 990).

A. campestris Nutt.—Common along Snake River (LW 1638, JFR 1452).

A. canescens Pursh.—Common in sagebrush flats of the valley (JFR 1369).

A. chilensis Nees. ssp. *adscendens* (Lindl.) Cronq.—Common on dry terraces above Pacific Creek (JFR 950).

A. conspicuus Lindl.—Common on the north side of Signal Mt. (JFR 2737).

A. coerulescens DC. var. *laetevirens* (Greene) Cron.—Common in the sedge grass meadow of the Wildlife Range (JFR 887).

A. engelmanni (D. C. Eaton) Gray.—Frequent around the shores of the valley lakes and in the major canyons up to 9000 ft. (RJS 1010, LW 921).
A. foliaceus Lindl. var. *apricus* A. Gray.—Infrequent in the lodgepole pine forest of the valley (JFR 1054).
A. foliaceus Lindl. var. *frondeus* A. Gray.—Common in the pothole area of the valley (JFR 1550).
A. integrifolius Nutt.—Common throughout the valley floor, also collected in the Lake Solitude area (LW 1707, JFR 2667).
A. occidentalis (Nutt.) T. & G. var. *typicus* Cron.—Common in the streamside forest (JFR 883).
Balsamorrhiza sagittata (Pursh.) Nutt.—Abundant in sagebrush flats and on moraines of the valley (RJS).
Bidens cernua L.—Common along west shore of upper Sawmill Pond, one mile south of Moose (RJS 759).
Brickellia grandiflora (Hook.) Nutt.—Frequent on the lower portions of the canyon trails (RJS 676).
Chaenactis alpina (Gray) Jones.—Infrequent on Skyline Trail above 9000 ft. (RJS 548).
C. douglasii (Hook.) H. & A.—Frequent along Snake River Bottom (LW 1150, JFR 2694).
Chrysopsis villosa (Hook.) Nutt.—Infrequent in the loose gravel of the Snake River (LW 1315, JFR 2526).
Chrysothamnus nauseosus (Pall.) Britt.—Abundant on the east side of the Snake River (JFR 2658).
Cirsium arvense L.—Common in waste places (JFR 1653).
C. drummondii T. & G.—Common in waste places throughout the valley (JFR 1330).
C. eatoni (Gray) Robinson.—Frequent in the talus slope of the major canyons (RJS 997).
Conyza canadensis (L.) Cronquist.—Infrequent in waste places (JFR 2538).
Crepis acuminata Nutt.—Infrequent in streambeds and under lodgepole pine (JFR 2245, LW 1240).
C. intermedia Gray.—Frequent in the big sagebrush areas of the Wildlife Range (JFR).
C. modocensis Greene.—Frequent in sagebrush, Sawmill Ponds area (RJS 620).
C. tectorum L.—Frequent along Snake River (JFR 2525).
Erigeron divergens T. & G.—Common in the sagebrush flats and the Snake River bottom (LW 1630).
E. eatoni Gray.—Frequent in rocks near Hidden Falls (LW 1104).
E. glabellus Nutt.—Frequent along the Snake River (JFR).
E. lonchophyllus Hook.—Infrequent along streams north of Moran (RJS 951).
E. ochroleucus Nutt.—Frequent in the sagebrush areas of the Wildlife Range (JFR).
E. peregrinus (Pursh.) Greene.—Frequent on the shores of alpine lakes above 9000 ft. (RJS 992, LW 1348).
E. pumilus Nutt.—Common in the sagebrush flats throughout the valley (RJS 908).
E. speciosus (Lindl.) DC. var. *macranthus* (Nutt.) Cronq.—Common in sagebrush flats and along the Snake River (LW 1331).
Eriophyllum lanatum (Pursh.) Forbes var. *integrifolium* (Hook.) Smiley.—Common in the sagebrush flats and on the moraines of the valley (RJS 532).
Gnaphalium palustre Nutt.—Common along Snake River (LW 1401, JFR 874).
Grindelia squarrosa (Pursh.) Duval.—Common in waste places (JFR 2531).
Haplopappus suffruticosus (Nutt.) Gray.—Infrequent two miles up Avalanche Canyon (RJS 688).
Helianthella quinquenervis (Hook.) Gray.—Locally common on morainal soil on the east shore of Jenny Lake, also in Wildlife Range (RJS 948, JFR 2841).
Helianthus annuus L.—Frequent in waste places and on the road to Two Ocean Lake (RJS).
Hieracium albiflorum Hook.—Frequent on trail west side of Jenny Lake (RJS 935).
H. cynoglossoides Arv.—Infrequent on slopes of Symmetry Spire and also in the lodgepole pine area of the Wildlife Range (RJS 971).
H. scouleri Hook.—Frequent in the sagebrush community, Wildlife Range (JFR 3018).
Iva xanthifolia Nutt.—Common in waste places (JFR 2648).

Lactuca integrata (Gren. & Godr.) A. Nels.—Frequent in streambeds and in waste places (JFR 2690).
L. pulchella (Pursh) D. C.—Infrequent along main highway just south of Timbered Island (RJS 873).
Madia glomerata Hook.—Locally common in waste places throughout the valley (RJS 940, JFR 1280).
Matricaria matricarioides (Less.) Porter.—Common in waste places throughout the valley (JFR 1279).
Microseris nutans (Geyer) Schultz.—Infrequent in Lupine Meadow south of Jenny Lake (RJS 623).
Rudbeckia occidentalis Nutt.—Locally frequent in moist areas around streams and lakes (RJS).
Senecio crassulus Gray.—Frequent in quaking aspen in area of Two Ocean Lake (LW 1647, JFR 2892).
S. crocatus Rydb.—Frequent in main couloir on the east face of Symmetry Spire, 9000 ft. (RJS 965, fide A. Cronq.).
S. cymbalarioides Nutt.—Frequent in the Wildlife Range (JFR).
S. hydrophilus Nutt.—Infrequent in the meadows of the Wildlife Range (JFR).
S. integerrimus Nutt.—Common in the sagebrush flats throughout the valley (RJS).
S. serra Hook.—Frequent on the dry bottoms of Cottonwood Creek (LW 1659).
S. triangularis Hook.—Common along streams in South Cascade Canyon (LW 1670).
Solidago ciliosa Greene.—Frequent south of Jenny Lake (RJS 531).
S. lepida DC. var. *fallfax* Fern.—Common under aspen on moist sites (JFR).
S. missouriensis Nutt.—Frequent in the streamside forest of the Wildlife Range (JFR).
S. multiradiata Ait.—Frequent along the Snake River and lower portions of the major canyons (LW 1645).
S. nana Nutt.—Dry hillside Cascade Canyon (LW 1683).
S. nemoralis Ait.—Common in the meadows around Moran (JFR).
Stephanomeria tenuifolia (Torr.) Hall.—Frequent on wet sand and rocky bars of the Snake River (LW 1321).
Tanacetum vulgare L.—Frequent along Snake River below Moran, remaining from previous cultivation (JFR 1654, RJS 1008).
Taraxacum officinale Weber.—Abundant throughout the valley.
Tetradymia inermis Nutt.—Locally common in the sagebrush of the valley floor (JFR 2961).
Tragopogon porrifolius L.—Frequent in waste places and sagebrush flats throughout the valley (RJS).
Viguiera multiflora (Nutt.) Blake.—Common along main highway throughout the valley (RJS 740).
Wyethia amplexicaulis Nutt.—Frequent along roadside, ¼ mile east of Moose on road to Elk, Wyo. (RJS 832).
W. helianthoides Nutt.—Frequent in moist meadow just south of Arizona Creek Guard Station (RJS 838).

Speciation in Cave Beetles of the Genus Pseudanophthalmus (Coleoptera, Carabidae)[1]

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The carabid cave fauna of North America has been known since the mid-nineteenth century through the work of Erichson (1844), Motschoulsky (1862), Leconte (1863), Horn (1868, 1871, 1883), Hubbard (1880), Garman (1892), and Barber (1928). Jeannel (1920) distinguished the North American genus *Pseudanophthalmus* from the European genus *Anophthalmus*. Jeannel's monograph of the Trechinae (1928) and his subsequent description (1931) of additional anophthalmid species collected by him in American caves encouraged an extensive study of this unique group by Valentine (1931, 1932, 1937, 1945, 1948, 1952).

It was felt that an extension of Valentine's excellent work, involving careful examination and analysis particularly of aedeagal structures, would provide further valuable information concerning the speciation pattern of this genus.

Acknowledgment.—The author wishes to express his gratitude to J. Manson Valentine whose standards of excellence in the study of American cavernicolous carabids have served as models for the present study and who gave valuable criticisms of the manuscript.

Methods and Materials

Collections were undertaken by the author beginning late in 1949. Trapping, using the methods described by Barber (1931), was tried rather extensively at first. But trapped specimens had often become disarticulated by the time the traps could be revisited. After some experience it was found that specimens could be found and seen most readily on moist mud flats where they could easily be taken with an aspirator. Since specimens were not taken by traps from caves in which they were not taken by hand, trapping operations were discontinued.

Collections were made in three Indiana caves and a Kentucky cave which are type localities of previously known Indiana forms and a closely related Kentucky form. Specimens were taken from seven other caves in the extensive cave area of south-central Indiana. Numerous other caves were also visited, some on several occasions, without specimens being found. Many others, relatively unknown and with difficult access, still remain to be visited.

For the sake of uniformity, measurements (in millimeters) and indices corresponding to those of Valentine (1932, 1945) were determined. These, with their abbreviations, are as follows:

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[1] Submitted in partial fulfillment of the degree of Doctor of Philosophy, Department of Zoology, University of Chicago. The author is indebted to Dr. Alfred E. Emerson for guidance and encouragement throughout this investigation.

L—LENGTH: length, measured in the median line, of the head and pronotum and elytra.

W—WIDTH: greatest width of the united elytra.

D—DEPTH: greatest median body depth.

w—WIDTH INDEX: width divided by total body length.

d—DEPTH INDEX: depth divided by total body length.

h—HEAD INDEX: greatest width of the head divided by head length.

p—PRONOTAL INDEX: greatest width of the pronotum divided by pronotum length.

e—ELYTRAL INDEX: greatest width of the united elytra divided by elytra length.

a—ANTENNAL INDEX: greatest length of the antenna divided by total body length.

s—ANTENNAL SEGMENTAL INDEX: "the greatest exposed length of the second antennal segment divided by the greatest exposed length of the third, measured dorsally" (Valentine, 1945).

c—CHAETOTAXIAL INDEX: "the distance, measured in a straight line, between the centers of the anterior and posterior marginal setiferous papillae of the humeral set of four, divided by the distance from the center of the fourth papilla to the center of the next more posterior marginal papilla" (Valentine, 1945).

g—GENITAL INDEX: "the longest chord of the arc subtended by the median lobe of the aedeagus measured between the extreme basal and apical extremities, divided by the total body length" (Valentine, 1945).

The descriptions are based on specimens degreased in ether. The figures were drawn by the author. Those of the elytral apex were made with the use of a microscope grid. The aedeagi dissected out for study have been placed into glycerin in small vials pinned with the specimens. The dorsal views (*in situ* orientation) were drawn of glycerin mounts, the lateral views of glycerin-jelly mounts, with the aid of a *camera lucida* attachment.

SPECIES DESCRIPTIONS

Group EREMITA

BODY: Size medium small to medium large (4.2-6.1 mm); elongate, moderately convex; from testaceous to dark ferrugino-testaceous; finely reticulo-alutaceous.

HEAD: Narrow; median tooth of labrum low, broad, poorly to fairly well defined.

PRONOTUM: Narrow; sides gently sinuate; posterior angles sharply rectangular, occasionally somewhat acute and produced; basal angles very obtuse or rounded, indistinct; basal margin shallowly concave; lateral reflexed margin rather wide; disc pilose to sparsely pubescent, convex.

ELYTRA: Narrow, convex, sparsely pubescent; humeri sloping slightly and rounded; sides gently arcuate, reflexed margin fairly wide, ciliate at humeri, sparsely ciliate throughout; apex obliquely truncate; striae fairly evident but weak on disc, obsolete laterally, vaguely but regularly punctured; recurved portion of apical stria short, usually joined to the third stria.

AEDEAGUS: Average aedeagus size of species in this group is proportional to the average body length of the species (average genital index 0.16-0.17), yet within each species aedeagus size is relatively constant no matter what the size of the specimen, hence a variable genital index in each species; median lobe elongated; viewed dorsally, strongly arched so that the basal flexure is extremely vague, widened near distal aperture which is subterminal, apex not produced; viewed laterally, robust, with conspicuous apical swelling; basal bulb large; basal plate well developed, terminal; transfer apparatus short, broad, composed of two plate-like copulatory pieces, the right one shorter, more broad, folded to partly enclose the left; parameres with three to five setae.

This group includes the only Indiana anophthalmids known heretofore. It is readily distinguished from other North American anophthalmids by the transfer apparatus of the aedeagus, these plate-like elements not being found

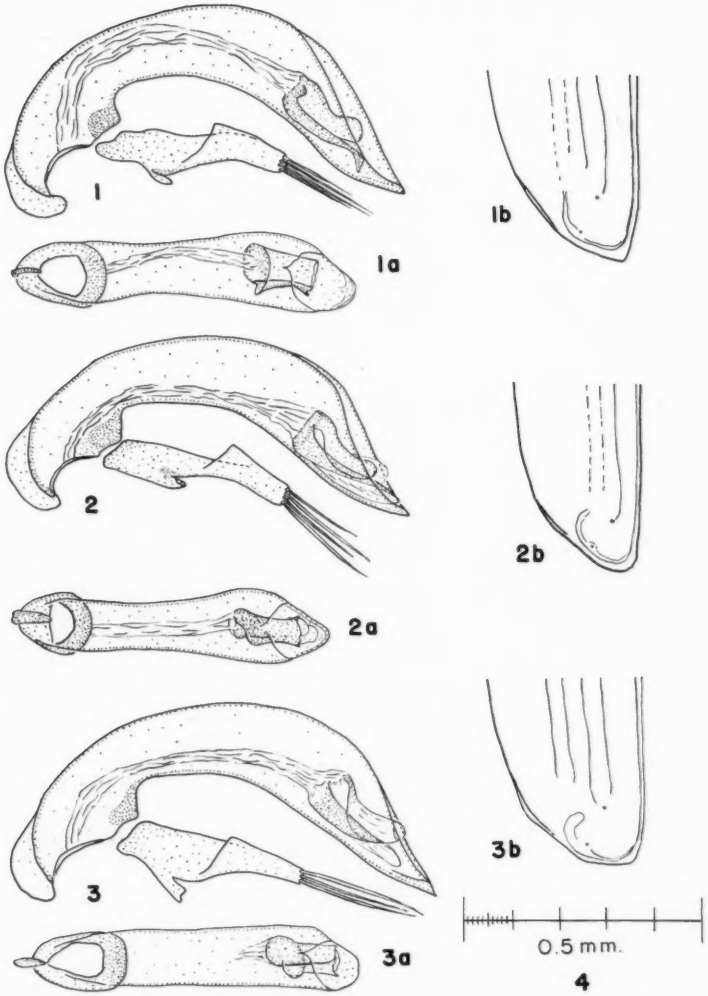

PLATE 1

Figs. 1-4.—1. *P. eremita,* plesiotype male; Wyandotte Cave, Crawford Co., Ind.; aedeagus, dorsal view. a—aedeagus, right lateral view. b—apical detail of left elytron. 2. *P. bloomi,* new species, holotype male; Langdon Cave, Harrison Co., Ind.; aedeagus, dorsal view. a—aedeagus, right lateral view. b—apical detail of left elytron. 3. *P. barberi,* plesiotype male; Morgan Cave, Meade Co., Ky.; aedeagus, dorsal view. a—aedeagus, right lateral view. b—apical detail of left elytron. 4. Scale for dorsal view of aedeagi.

elsewhere. By means of this apparatus it is also distinguished from the other Indiana groups.

Several body characters separate it from the other Indiana groups. The recurved portion of the apical stria joins or tends to join the third stria, rather than the fifth as in other groups. The posterior angles of the pronotum are sharply rectangular, little produced, as compared to the acute, produced angles of other groups. The median tooth of the labrum is broader and less well defined than in the other groups.

PSEUDANOPHTHALMUS EREMITA (Horn)

Anophthalmus eremita Horn 1871:325. Horn 1883:272. Packard 1886:75. Leng and Mutchler 1920:55.

A. tenuis Horn 1871:327. Horn 1883:272. Packard 1886:75.

Pseudanophthalmus eremita; Jeannel 1928:131.

P. eremita eremita; Jeannel 1931:466. Valentine 1932:275. Jeannel 1949:56.

Type locality.—Wyandotte Cave, five miles northeast of Leavenworth, Crawford Co., Ind.

Holotype.—Acad. Nat. Sci. Phila.

Topotype series.—Plesiotype male and twenty topotypes; Aug. 4, 1950; C. H. K.

Plesiotype male (Chi. Nat. Hist. Mus.) (Plate 1, fig. 1).—Aug. 4, 1950; C. H. K.; L—5.88; W—1.85; D—1.11; w—0.31; d—0.19; h—0.55; p—1.11; e—0.57; a—0.59; s—0.70; c—0.44; g—0.15.

P. eremita, the first Indiana anophthalmid to be described, is intermediate in the size range of group *eremita,* averaging 5.32 ± 0.07 mm in length. Corresponding to its intermediate body size is its intermediate aedeagus size (five specimens had range 0.82-0-89, mean 0.84 mm). It ranges in color from pale to dark ferrugino-testaceous. The recurved portion of the apical stria is short, straight or weakly sinuate (plesiotype), subparallel to the suture, with a weak or no apparent (plesiotype) connection to the third stria. The left copulatory piece of the aedeagus viewed dorsally is distinctly longer than the right, is subapically constricted, and is apically flared and deflected sinistrally; this piece is short (0.27 the length of the median lobe).

Species of group *eremita* to the north, *stricticollis, jeanneli,* and *morrisoni,* are similar in being of larger size and having a left copulatory piece which is like that in *eremita.* Species of group *eremita* to the south, *bloomi* and *barberi,* are similar in being of smaller size and possessing a left copulatory piece not constricted subapically.

Wyandotte Cave is a commercialized cave, the largest and best known in Indiana, and one of the larger American caves. *Pseudanophthalmus* was taken both at the Throne Room and at Crayfish Spring, though it may very well be more extensively scattered through the cave. The cave lies to the west of the Blue River into which its streams presumably drain.

PSEUDANOPHTHALMUS STRICTICOLLIS (Jennnel)

Pseudanophthalmus eremita stricticollis Jeannel 1931:468. Valentine 1932:275. Jeannel 1949:56.

Type locality.—Marengo Cave, Marengo, Crawford Co., Ind.

Holotype.—coll. Jeannel.

Topotype series.—Plesiotype male and nine topotypes; Aug. 5, 1950; C. H. K.

Plesiotype male (Chi. Nat. Hist. Mus.) (Plate 2, fig. 1).—Aug. 5, 1950; C. H. K.; L—5.77; W—1.85; D—1.15; w—0.32; d—0.20; h—0.58; p—1.15; e—0.57; a—0.65; s—0.73; c—0.42; g—0.16.

P. stricticollis is distinctly longer than *eremita*, its average length being 5.63 ± 0.10 mm. Correspondingly the aedeagus size is larger (five specimens had range 0.90-0.94, mean 0.91 mm). In color it is darker than *eremita*, ranging from medium to dark ferrugino-testaceous. The recurved portion of the apical stria, somewhat shorter than in *eremita*, is sinuate, subparallel to the suture, with a weak (plesiotype) or no apparent connection to the third stria. The copulatory pieces of the aedeagus are subequal in length, and the left piece is subapically constricted and deflected sinistrally; this piece is short, as in *eremita*.

Marengo is a well-known commercialized cave. Most of the specimens captured were taken in that portion of the cave with the greatest traffic, walking along the paths and crawling over lighted formations. The stream near which it lies flows into the Blue River.

Pseudanophthalmus jeanneli n. sp.

Type series.—Holotype, allotype, and one paratype; Elrod's Cave, two miles east of Orangeville, Orange Co., Ind.; Aug. 12, 1950; C. H. K., W. W. Bloom.

Holotype male (Chi. Nat. Hist. Mus.) (Plate 2, fig. 2).—L—5.85; W—2.00; D—1.15; w—0.34; d—0.20; h—0.63; p—1.17; e—0.61; a—0.65; s—0.78; c—0.41; g—0.16.

Allotype female (Chi. Nat. Hist. Mus.).—L—4.66; W—1.59; D—0.96; w—0.34; d—0.21; h—0.67; p—1.17; e—0.62; a—0.67; s—0.78; c—0.51.

The three specimens in this series vary considerably in size (their range in length is 4.66-5.85, mean 5.32 mm). Moreover, the measurements of the two aedeagi, 0.88 and 0.96 mm, are not too accurate because both male specimens were tenerals. The two males are pale, the female medium, ferrugino-testaceous. *P. jeanneli* is distinguished from *stricticollis* as follows: the recurved portion of the apical stria is shorter, arcuate, curving throughout its length to the third stria; the left element of the transfer apparatus, subapically constricted and deflected sinistrally, is considerably longer than the right element and is long relative to the length of the median lobe (0.33 its length).

Elrod's Cave is but one of the many caves known to lie along the complex underground drainage system of the Lost River which "rises" at Orangeville. It is a pleasure to name the form described above in honor of Dr. R. Jeannel whose monograph of the Trechinae and study of the carabid cave fauna of North America are basic to current investigations of this fauna.

PSEUDANOPHTHALMUS MORRISONI (Jeannel)

Pseudanophthalmus eremita morrisoni Jeannel 1931:468. Valentine 1932:275. Jeannel 1949:56.

Type locality.—Donnelson's or Donaldson's Cave, four miles east of Mitchell, Lawrence Co., Ind.

Holotype.—coll. Jeannel.

Topotype series.—Plesiotype male and eleven topotypes; June 16, 1950; Aug. 11, 1950; Nov. 4, 1950; Nov. 9, 1953; C. H. K.

Plesiotype male (Chi. Nat. Hist. Mus.) (Plate 2, fig. 3).—June 16, 1950; C. H. K.; L—6.07; W—2.04; D—1.15; w—0.34; d—0.19; h—0.57; p—1.21; e—0.61; a—0.60; s—0.79; c—0.46; g—0.16.

P. morrisoni is the largest species in group *eremita* (its average length is 5.67 ± 0.12 mm) though it overlaps considerably with *stricticollis* and *jeanneli* (its range is 4.85-6.07 mm). Aedeagus length of the six measured

is 0.90-1.01, mean 0.98 mm, only one overlapping the range of *stricticollis* and *jeanneli*. The color ranges from pale to dark ferrugino-testaceous. The pronotum is wider than in all other species of the group; its pronotal index is 1.12-1.48, mean 1.22, as compared to an average of 1.14 or 1.15 in the other species. The recurved portion of the apical stria is short, gently arcuate, subparallel to the suture at the level of the fourth stria, and curves rather sharply proximally to the third stria, rather than throughout its length as in *jeanneli*. The left element of the transfer apparatus, subapically constricted and deflected sinistrally, is longer than the right element; its length relative to that of the median lobe (0.30 its length) is greater than in *stricticollis* and *eremita*, less than in *jeanneli*.

This form was taken from a complex of caves, called hereafter the Donaldson complex, known by actual exploration to be interconnected. This complex includes Donaldson's or Donnelson's Cave, Bronson's Cave, and the upper and lower Twin Caves. The stream issuing from the mouth of Donaldson's Cave drains via Mill Creek north to the east fork of the White River.

Anophthalmids were found abundantly on mud flats along the stream of the upper Twin Cave. These have proven to be of two distinct species, *morrisoni* and *donaldsoni*, both species being found on the same flats.

Pseudanophthalmus bloomi n. sp.

Type series.—Holotype, allotype, and three paratypes; Langdon Cave, three miles southwest of White Cloud, Harrison Co., Ind.; Aug. 11, 1950; C. H. K., W. W. Bloom.

Holotype male (Chi. Nat. Hist. Mus.) (Plate 1, fig. 2).—L—4.55; W—1.55; D—1.00; w—0.34; d—0.22; h—0.67; p—1.13; e—0.60; a—0.70; s—0.83; c—0.47; g—0.17.

Allotype female (Chi. Nat. Hist. Mus.).—L—4.48; W—1.55; D—1.04; w—0.35; d—0.23; h—0.62; p—1.14; e—0.63; a—0.64; s—0.82; c—0.47.

P. bloomi is distinctly smaller on the average than *eremita*, its average length being 4.80 ± 0.12 mm. The two aedeagi measured are 0.78 and 0.86 mm, the former lower than the range but the latter higher than the average of *eremita*. The color ranges from medium to dark ferrugino-testaceous. Characters distinguishing *bloomi* from *eremita* are: recurved portion of apical stria is short, arcuate, curving inward along its entire length, vaguely or not (holotype) connected to third stria; the left element of the transfer apparatus is not subapically constricted, the entire element tapering abruptly to a blunt point, distinctly longer than the right element. The chaetotaxial index (0.42-0.52, mean 0.48) is somewhat higher than in *eremita* (0.41-0.50, mean 0.44) and other species to the north (*stricticollis*, 0.37-0.47, mean 0.42; *jeanneli*, 0.41-0.51, mean 0.45; *morrisoni*, 0.41-0.48, mean 0.45).

Though Langdon's Cave is less than five miles from Wyandotte Cave, *bloomi* is quite distinct from *eremita*. The cave is high above the level of the Ohio, to the east of the Blue River near which it lies. The author takes pleasure in naming the above described form after Dr. William W. Bloom of Valparaiso University, a colleague who capably assisted in the capture of this and other species of cave beetles.

PSEUDANOPHTHALMUS BARBERI (Jeannel)

Pseudanophthalmus barberi Jeannel 1928:133. Jeannel 1949:58.

P. eremita barberi Jeannel 1931:468. Valentine 1932:275.

Type locality.—Rockhaven Cave, eight miles east-by-northeast of Brandenburg, Meade Co., Ky.

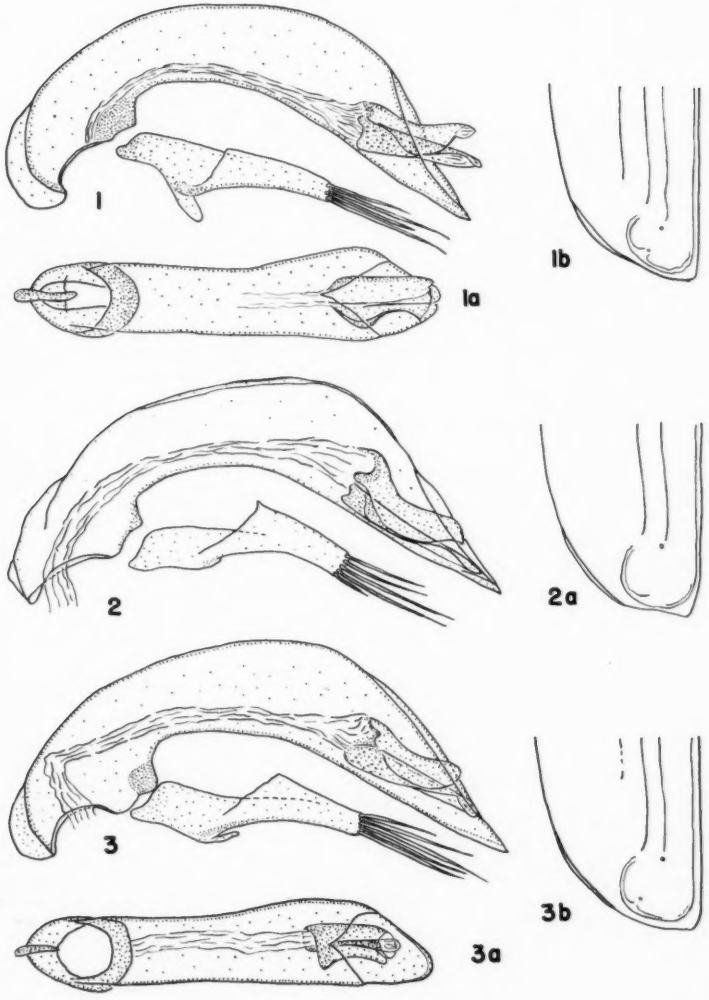

PLATE 2

Figs. 1-3.—1. *P. stricticollis,* plesiotype male; Marengo Cave, Crawford Co., Ind.; aedeagus, dorsal view. a—aedeagus, right lateral view. b—apical details of left elytron. 2. *P. jeanneli,* new species, holotype male; Elrod's Cave, Orange Co., Ind.; aedeagus, dorsal view. a—apical detail of left elytron. 3. *P. morrisoni,* plesiotype male; Donaldson's Cave, Lawrence Co., Ind.; aedeagus, dorsal view. a—aedeagus, right lateral view. b—apical detail of left elytron.

Holotype.—U. S. N. M.

Topotype series.—Plesiotype male and thirty-six topotypes; Aug. 19, 1953; C. H. K., P. Johnson.

Plesiotype male (Chi. Nat. Hist. Mus.) (Plate 1, fig. 3).—L—5.25; W—1.81; D—0.96; W—0.34; d—0.18; h—0.64; p—1.15; e—0.61; a—0.65; s—0.73; c—0.51; g—0.16.

P. barberi is very similar to *bloomi*. Like *bloomi* it is considerably smaller than *eremita* (its mean length is 4.83 ± 0.05 mm). The aedeagus size is correspondingly low, the seven measured being 0.71-0.84, mean 0.77 mm. The color ranges from testaceous to medium ferrugino-testaceous. The recurved portion of the apical stria is very short, straight or gently arcuate (not as bowed as in *bloomi*), parallel to the suture at the level of the fourth stria, vaguely or not (plesiotype) connected to the third stria. More sharply distinguishing it from *bloomi* is the fact that the copulatory pieces are subequal in length (in *bloomi* the left is distinctly longer); the left piece as in *bloomi* is not subapically constricted. The chaetotaxial index in this species ranges more widely and averages higher (0.44-0.64, mean 0.52) than in any other species of group *eremita*.

At Rock Haven, eight miles north and east of Brandenburg, Kentucky, are two caves, Morgan's and Jesse James', which lie about half a mile apart. Which of these is the type cave cannot be determined. Careful comparison of the series from the two caves failed to reveal any distinguishing characteristics between them, hence they are described as one form. Both caves lie on a high bluff along the Ohio River toward which the small stream of each flows directly; underground channels may well interconnect the two caves.

Group YOUNGI

BODY: size medium (4.3-5.4 mm); elongate, moderately convex; from testaceous to dark ferrugino-testaceous; finely reticulo-alutaceous.

HEAD: narrow; median tooth of labrum low, rather narrow, fairly well to well defined.

PRONOTUM: narrow; sides gently sinuate; posterior angles acute, somewhat produced; basal angles very obtuse or rounded, indistinct; basal margin straight to shallowly concave; lateral reflexed margin narrow; disc pilose, convex.

ELYTRA: narrow, convex, sparsely pubescent; humeri sloping slightly, with fairly distinct angles; sides very gently arcuate, reflexed margin fairly wide, ciliate throughout, more regularly at humeri and along posterior half; apex obliquely truncate; striae barely evident on disc, obsolete laterally, very vaguely but regularly punctured; recurved portion of apical stria directed toward fifth stria.

AEDEAGUS: size roughly equivalent (1 mm ±), no matter how large or small the specimen, hence a variable genital index (0.19-0.23); median lobe stout; viewed dorsally, very strongly arched dextrally so that the basal flexure is extremely vague, weakly arcuate sinistrally, distal aperture subterminal, apex not produced; viewed laterally, robust, sides weakly sinuate, of equal width throughout; basal bulb large; basal plate present, terminal; transfer apparatus long, composed of two copulatory pieces, subequal in length, difficult to interpret; the left ventral element a long rod, broad at its base and somewhat pointed apically, the right dorsal element a long broad spatula somewhat folded at its base; internal sac armed with many rows of small barbs; parameres with four to six setae.

Diagnostic is the aedeagus, especially the transfer apparatus. Externally it shares with groups *shilohensis* and *emersoni* characters which separate them from group *eremita*: sharper, more produced, posterior pronotal angles; narrower, better defined, median labral tooth; recurved portion of apical stria directed toward the fifth stria. The elytra of this group are most gently

arcuate, almost parallel, and the angles of the humeri are fairly distinct. The elytral striae are barely evident as compared to groups *eremita* and *shilohensis;* the reflexed margins of the elytra are ciliate throughout, as compared to those of group *emersoni* which are ciliate only at the humeri.

Pseudanophthalmus youngi n. sp.

Type series.—Holotype, allotype, and seventeen paratypes; Clifty Caves, four miles north of Campbellsburg, Washington Co., Ind.; June 17, 1950; C. H. K.

Holotype male (Chi. Nat. Hist. Mus.) (Plate 3, fig. 1).—L—5.07; W—1.70; D—1.22; w—0.34; d—0.24; h—0.63; p—1.12; e—0.61; a—0.60; s—0.74; c—0.45; g—0.20.

Allotype female (Chi. Nat. Hist. Mus.).—L—4.74; W—1.59; D—1.00; w—0.34; d—0.21; h—0.59; p—1.22; e—0.63; a—0.59; s—0.82; c—0.44.

P. youngi is very similar to *donaldsoni,* being distinguished from it with difficulty. The depth of the *youngi* series averages 1.12 ± 0.02 mm, that of the *donaldsoni* series 1.02 ± 0.02 mm. The depth index also shows *youngi* to be deeper relative to its length; its index is 0.20-0.26, mean 0.23, while that of *donaldsoni* is 0.18-0.24, mean 0.21. In *youngi* the apical stria tends to follow the apical margin laterally quite some distance before curving anteriorly in a weakly sinuate line, first subparallel to the suture, then laterally to the fifth stria. The aedeagus of *youngi,* viewed dorsally, is somewhat thinner in outline than in *donaldsoni,* and the basal bulb is not produced downward as extensively (the aedeagi of the type specimens show this distinction less clearly than those of paratypes examined).

Two caves, known as the wet and dry Clifty Caves, open within two hundred yards of one another at the head of a deep and narrow valley. Small passageways may well connect them. No distinction can be made between the forms from the two caves, and they are considered a single species. The streams emerging from the caves form Clifty Creek which flows northwesterly to the east fork of the White River.

The author takes great pleasure in naming this species after Dr. Frank N. Young of Indiana University who gave advice and encouragement during the course of this investigation.

Pseudanophthalmus donaldsoni n. sp.

Type series.—Holotype, allotype, and thirty-four paratypes; Donaldson Cave complex (Donaldson's Cave, Twin Caves, Bronson's Cave), four miles east of Mitchell, Lawrence Co., Ind., June 16, 1950; Aug. 11, 12, 1950; Nov. 9, 1953; C. H. K.

Holotype male (Chi. Nat. Hist. Mus.) (Plate 3, fig. 2).—Aug. 12, 1950; C. H. K.; L—5.22; W—1.81; D—1.15; w—0.35; d—0.22; h—0.71; p—1.15; e—0.62; a—0.63; s—0.76; c—0.42; g—0.19.

Allotype female (Chi. Nat. Hist. Mus.).—Nov. 9, 1953; C. H. K.; L—5.00; W—1.63; D—0.96; W—0.33; d—0.19; h—0.58; p—1.16; e—0.61; a—0.59; s—0.74; c—0.43.

P. donaldsoni is distinguished from *youngi* as follows: its body is less deep; the apical stria tends to follow the apical margin less laterally before curving anteriorly, in a straight or weakly sinuate line, laterally to the fifth stria; the median lobe of the aedeagus, viewed dorsally, is somewhat thicker in outline, and the basal bulb is produced further downward.

P. donaldsoni is found in the Donaldson complex side by side with *morrisoni. P. donaldsoni* is the more numerous species.

Group EMERSONI

Pseudanophthalmus emersoni n. sp.

Type series.—Holotype, allotype, and four paratypes; Donnehue's Cave, one mile southwest of Bedford, Lawrence Co., Ind., Aug. 13, 1950, C. H. K., W. W. Bloom; Nov. 9, 1953, C. H. K.

Holotype male (Chi. Nat. Hist. Mus.) (Plate 3, fig. 3).—Nov. 9, 1953; C. H. K.; L—4.59; W—1.55; D—0.85; w—0.34; d—0.19; h—0.69; p—1.13; e—0.61; a—0.61; s—0.78; c—0.44; g—0.17.

Allotype female (Chi. Nat. Hist. Mus.).—Aug. 13, 1950; C. H. K., W. W. Bloom; L—4.44; W—1.52; D—0.92; w—0.34; d—0.21; h—0.64; p—1.09; e—0.64; a—0.56; s—0.81; c—0.54.

BODY: size small (3.8-4.9 mm); elongate, moderately convex; ferrugino-testaceous; finely reticulo-alutaceous.

HEAD: narrow; median tooth of labrum fairly well defined.

PRONOTUM: narrow; sides gently sinuate; posterior angles acute, slightly produced; basal angles very obtuse or rounded, indistinct; basal margin concave in entirety but with a medial convexity which is so extensive in two (teneral?) specimens that the margin appears convex; lateral reflexed margin narrow; disc pilose to sparsely pubescent, convex.

ELYTRA: narrow, convex; humeri sloping slightly, with vaguely defined angles; sides gently arcuate, reflexed margin fairly wide, ciliate at humeri; apex obliquely truncate; striae barely evident on disc, obsolete laterally, very vaguely and irregularly punctured; recurved portion of apical stria short, straight, parallel to suture; pubescence rather long and sparse; a remarkably wide range (0.44-0.74) and a high average (0.56) in the chaetotaxial index.

AEDEAGUS: medial lobe elongate; viewed dorsally, well arched so that the basal flexure is vague, slightly narrowed near distal aperture which is subterminal, apex not produced; viewed laterally, rather slender, sides fairly straight, equally wide throughout; basal bulb not large; basal plate present, terminal; transfer apparatus fairly long, composed of two copulatory pieces, the left one a short pointed style, lying within the right one, a long, broad spatula with inwardly curled margins; internal sac armed with many rows of small barbs; parameres elongate, with five setae.

P. emersoni is most readily distinguished by the transfer apparatus of the aedeagus. Externally it shares with groups *youngi* and *shilohensis* characters which separate them from group *eremita*: sharper, more produced posterior pronotal angles; narrower, better defined, median labral tooth; recurved portion of apical stria directed toward the fifth stria. It is distinguished from all other Indiana groups by its lack, except at the humeri, of cilia along the reflexed margin of the elytra.

Donnehue's Cave lies within a bluff only several hundred yards from the east fork of the White River into which the stream which flows from its mouth rapidly descends. The author takes great pleasure in naming this species in honor of Dr. Alfred E. Emerson of the University of Chicago who has given much encouragement to this study.

Group SHILOHENSIS

BODY: size medium (4.5-5.2 mm); elongate, moderately convex; from medium to dark ferrugino-testaceous; finely reticulo-alutaceous.

HEAD: narrow; median tooth of labrum fairly well defined.

PRONOTUM: narrow; sides gently sinuate; posterior angle apices sharp and somewhat produced; basal angles very obtuse or rounded, indistinct; basal margin shallowly concave; lateral reflexed margin narrow; disc sparsely pubescent to pilose, convex.

ELYTRA: narrow, convex, sparsely pubescent; humeri sloping slightly, with vaguely defined angles; sides gently arcuate; reflexed margin fairly wide, ciliate at humeri, sparsely ciliate throughout; apex obliquely truncate; striae evident but weak on disc, less distinct

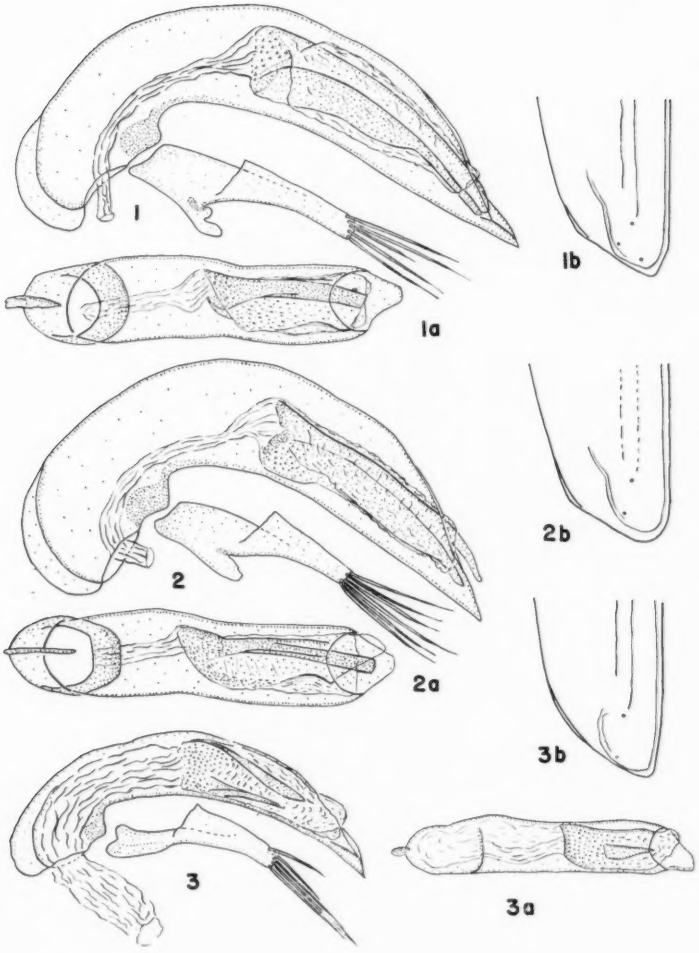

PLATE 3

Figs. 1-3.—1. *P. youngi,* new species, holotype male; Clifty Cave, Washington Co., Ind.; aedeagus, dorsal view. a—aedeagus, right lateral view. b—apical detail of left elytron. 2. *P. donaldsoni,* new species, holotype male; Donaldson Cave Complex, Lawrence Co., Ind.; aedeagus, dorsal view. a—aedeagus, right lateral view. b—apical detail of left elytron. 3. *P. emersoni,* new species, holotype male; Donnehue's Cave, Lawrence Co., Ind.; aedeagus, dorsal view. a—aedeagus, right lateral view. b—apical detail of left elytron.

laterally, very vaguely but regularly punctured; recurved portion of apical stria fairly long, directed toward or beyond the fifth stria.

AEDEAGUS: size proportional to body size, with a genital index of 0.18; median lobe elongate; viewed dorsally, flattened sinistrally, but well arched dextrally so that basal flexure is vague, widest proximal to the distal aperture which is subterminal, apex slightly produced; viewed laterally, rather slender, sides fairly straight, slightly enlarged at the basal bulb; basal bulb fairly large; basal plate present, terminal; transfer apparatus fairly long, consisting of a broad spatulate structure spirally twisted, whose edges overlap proximally so that a spout is formed; internal sac armed with many rows of small barbs; parameres elongate, bearing three to five setae.

This group is most readily recognized by the transfer apparatus of the aedeagus. Externally it shares with groups *youngi* and *emersoni* characters which separate them from group *eremita*: sharper, more produced posterior pronotal angles; narrower, better defined, median labral tooth; recurved portion of apical stria directed toward the fifth stria. It is distinguished from groups *shilohensis* and *emersoni* by its long recurved portion of the apical stria.

Pseudanophthalmus shilohensis n. sp.

Type series.—Holotype, allotype, and six paratypes; Shiloh Cave, six miles west-by-northwest of Bedford, Lawrence Co., Ind., Dec. 11, 1949; Dec. 11, 1949 to June 18, 1950, trapped; June 18, 1950; C. H. K.

Holotype male (Chi. Nat. Hist. Mus.) (Plate 4, fig. 1).—Dec. 11, 1949; C. H. K.; L—4.97; W—1.63; D—0.89; w—0.33; d—0.18; h—0.57; p—1.08; e—0.60; a—0.57; s—0.78; c—0.52; g—0.18.

Allotype female (Chi. Nat. Hist. Mus.).—June 18, 1950; C. H. K.; L—4.74; W—1.55; D—0.96; w—0.33; d—0.20; h—0.65; p—1.08; e—0.60; a—0.59; s—0.83; c—0.46.

P. shilohensis has a narrower pronotum than either *mayfieldensis* or *boonensis;* its pronotal index is 1.04-1.09, mean 1.07, that of *mayfieldensis* 1.08-1.17, mean 1.13, that of *boonensis* 1.09-1.23, mean 1.14. The recurved portion of the apical stria is parallel to the suture for half its length, beyond which point it curves fairly sharply laterally beyond the fifth stria. The humeral set of the marginal setae are more widely separated from the fifth papilla than in the other members of the group; its chaetotaxial index is 0.43-0.52, mean 0.47, that of *mayfieldensis* 0.39-0.47, mean 0.42, that of *boonensis* 0.39-0.45, mean 0.42.

The opening through which access is had to Shiloh Cave lies at the bottom of a large sink hole. Through the cave flows a good sized stream which exits less than a mile to the south from where it flows into Salt Creek which in turn joins the east fork of the White River.

Pseudanophthalmus mayfieldensis n. sp.

Type series.—Holotype, allotype, and three paratypes; Mayfield's Cave, five miles west-by-northwest of Bloomington, Monroe Co., Ind.; Nov. 4, 1950; Nov. 3, 1951; C. H. K.

Holotype male (Chi. Nat. Hist. Mus.) (Plate 4, fig. 2).—Nov. 3, 1951; C. H. K.; L—5.00; W—1.74; D—1.15; w—0.35; d—0.23; h—0.68; p—1.11; e—0.67; a—0.66; s—0.81; c—0.42; g—0.18.

Allotype female (Chi. Nat. Hist. Mus.).—Nov. 3, 1951; C. H. K.; L—5.22; W—1.70; D—1.11; w—0.33; d—0.21; h—0.61; p—1.08; e—0.60; a—0.60; s—0.75; c—0.40.

P. mayfieldensis resembles *boonensis* very closely, having a similar pronotal index (1.13 and 1.14 respectively) and chaetotaxial index (each 0.42).

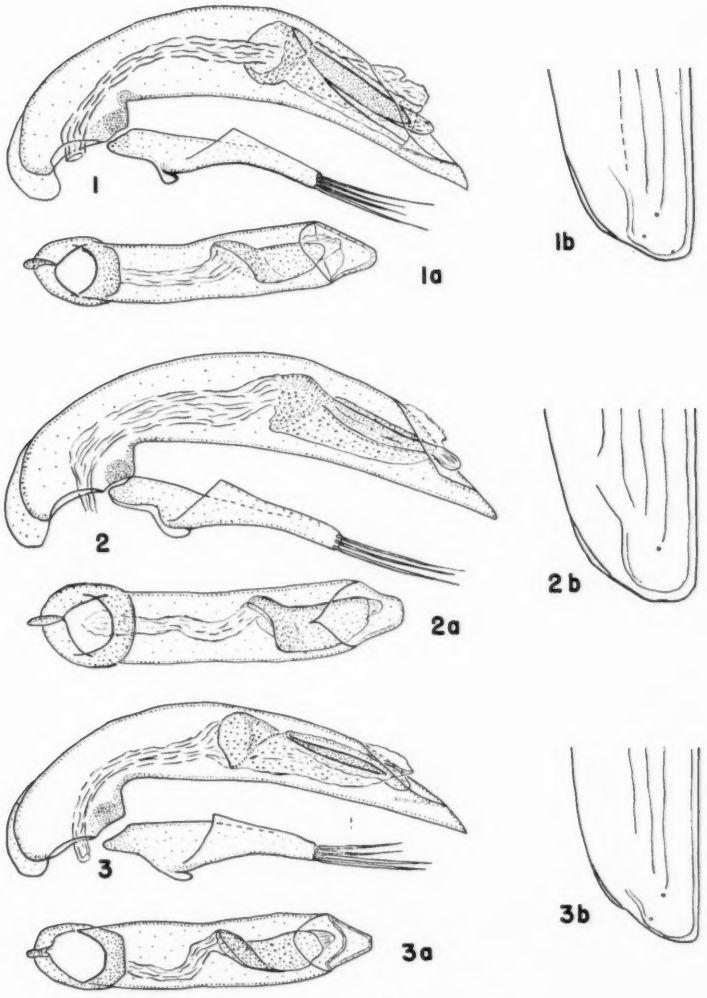

PLATE 4

Figs. 1-3.—1. *P. shilohensis*, new species, holotype male; Shiloh Cave, Lawrence Co., Ind.; aedeagus, dorsal view. a—aedeagus, right lateral view. b—allotype female, apical detail of left elytron. 2. *P. mayfieldensis*, new species, holotype male; Mayfield's Cave, Monroe Co., Ind.; aedeagus, dorsal view. a—aedeagus, right lateral view. b—allotype female, apical detail of left elytron. 3. *P. boonensis*, new species, holotype male; Boone Cave, Owen Co.; aedeagus, dorsal view. a—aedeagus, right lateral view. b.—allotpye female, apical detail of left elytron.

In both the recurved portion of the apical stria is fairly long, gently sigmoid, extending laterally beyond the fifth stria. In these respects both differ from *shilohensis*. *P. mayfieldensis* differs from *boonensis* in the form of the median lobe of aedeagus, viewed dorsally: in *mayfieldensis*, as well as *shilohensis*, the tube is expanded to a considerable extent midway along its length; in *boonensis* this expansion is very slight, so that the tube is more slender in its outline.

Mayfield Cave is that cave studied intensively in the classical investigation of Banta (1907). The small stream of the cave presumably drains into Richland Creek near which it lies, though the drainage pattern in this area is extremely complex because of the subsurface channels; Richland Creek flows into the north fork of the White River. Several collecting trips and extensive trapping were conducted in the cave before specimens were taken by hand in the side passage near the mouth.

Pseudanophthalmus boonensis n. sp.

Type series.—Holotype, allotype, and one paratype; Boone Cave, one mile north of Freeman, Owen Co., Ind.; July 22, 1950; July 31, 1950; Nov. 5, 1950; C. H. K.

Holotype male (Chi. Nat. Hist. Mus.) (Plate 4, fig. 3).—July 22, 1950; C. H. K.; L—4.74; W—1.48; D—0.85; w—0.31; d—0.18; h—0.56; p—1.23; e—0.57; a—0.54; s—0.81; c—0.45; g—0.18.

Allotype female (Chi. Nat. Hist. Mus.).—Nov. 5, 1950; C. H. K.; L—4.52; W—1.44; D—0.89; w—0.32; d—0.20; h—0.59; p—1.09; e—0.57; a—0.57; s—0.87; c—0.43.

P. boonensis and *mayfieldensis* are very similar in respect to pronotal index, chaetotaxial index, and in the appearance of the recurved portion of the apical stria. *P. boonensis* differs from *mayfieldensis* and *shilohensis* in that the median lobe of the aedeagus, viewed dorsally, is only slightly expanded, so that the tube has a slender outline.

Boone Cave is quite small. Several intensive searchings along low passageways where mud and muddy gravel exists, and trapping at these places, resulted in three specimens being taken, all by hand. The stream flowing from its mouth joins Raccoon Creek which drains into the north fork of the White River.

DISCUSSION

SPECIATION AND DISTRIBUTION

An extremely interesting problem that arises as the speciation pattern of *Pseudanophthalmus* becomes more completely known concerns the distribution of these organisms. The facts presented by Valentine (1931, 1932, 1937, 1945, 1948) have no simple explanation. In most cases his data suggest that speciation has occurred as forms dispersed along river valleys have become isolated; usually those forms within a given drainage system are most closely related. Within such groups (for example, in what he describes as polytypic *lodingi* and *hubbardi*) taxonomic relatedness is quite closely correlated with geographic proximity measured along interconnecting streams rather than overland. In these cases small streams or rivers appear not to constitute barriers to distribution, while mountains and land masses do. There are, however, several important exceptions to this pattern. There are cases in which very closely related forms are separated by considerable geographic distances; for example, approximately two hundred miles separate

engelhardti from *lodingi*, which forms are so closely related that Valentine would call them subspecies if it were not for this distance separating them. There are cases in which closely related forms are found along drainage systems on both sides of a divide; for example, polytypic *hubbardi* is found along branches of the Potomac River which drains toward the Atlantic, while closely related *grandis* and *fuscus* are found along the Greenbrier River which drains into the Ohio.

The data presented in this paper would appear to constitute additional exceptions to a simple pattern of dispersal along present river valleys. Especially the distribution pattern of the species of group *eremita* (Plate 5) is exceptional. The species of this group differ from one another to about the same extent as those forms which Valentine describes as subspecies. Yet very closely related *jeanneli*, *stricticollis*, and *morrisoni* (Plate 2), though separated from one another overland by only ten to thirty miles, are separated

PLATE 5

Map showing anophthalmid fauna distribution in southern Indiana and northern Kentucky. Group *Eremita:* 1. *P. eremita*, 2. *P. bloomi*, 3. *P. barberi*, 4. *P. stricticollis*, 5. *P. jeanneli*, 6. *P. morrisoni*. Group *Youngi:* 7. *P. donaldsoni*, 8. *P. youngi*. Group *Emersoni:* 9. *P. emersoni*. Group *Shilohensis:* 10. *P. shilohensis*, 11. *P. boonensis*, 12. *P. mayfieldensis*.

by extremely large distances as measured along stream courses (*morrisoni* to *jeanneli, ca.* 100 miles; *morrisoni* to *stricticollis, ca.* 420 miles; *jeanneli* to *stricticollis, ca.* 400 miles). Very closely related *bloomi* and *barberi* (Plate 1) are separated by some twenty miles and are found on different sides of the large Ohio River. On the other hand, *stricticollis, eremita,* and *bloomi,* found in caves separated by no more than fifteen miles and lying along streams flowing into the Blue River, are more distantly related (Plates 1 and 2).

Likewise the distribution patterns of the species of group *shilohensis* is exceptional (Plate 5). These very closely related species (Plate 4), separated from one another overland by seven to thirty miles, are separated by quite large distances as measured along stream courses (*boonensis* to *mayfieldensis, ca.* 60 miles; *boonensis* to *shilohensis, ca.* 160 miles; *mayfieldensis* to *shilohensis, ca.* 160 miles).

The relatedness of forms endemic to a drainage system is most readily accounted for by dispersal along stream valleys. But how are the exceptional distributions such as those cited above to be explained?

One possibility to be considered is that dispersal is by way of underground channels not parallel to surface drainage. Valentine (1932) proposes such a route to account for the presence of *alabamae* on the Coosa River drainage on the other side of Lookout Mountain from which are found closely related species of group *engelhardti* along the Tennessee River drainage. There is considerable underground drainage in southern Indiana where the present study was made. In fact, Elrod's Cave, the type locality of *jeanneli,* comprises a portion of the underground Lost River system whose extent and complexity has been described by Malott (1932, 1949, 1952). The headwaters of this system, however, draining an area of fifty-three square miles lying between the type localities of *morrisoni, stricticollis,* and *jeanneli* form a normal dendritic system with little evidence of underground drainage (Malott, 1952). Should underground channels exist, connecting these specific localities or any others, they would seem to be recently developed, more likely to be involved in providing interconnecting channels for two previously isolated species than in providing avenues of dispersal for populations now isolated.

A second possibility is that dispersal is overland across divides. This might appear unlikely on first thought, for one might feel that organisms like these, known to occur only in a constant, cool, humid cave environment, would find it impossible to be dispersed any great distance in an environment unlike that to which they are accustomed. It seems that some such dispersal, however, would most readily account for the present distribution of the species of group *shilohensis* and of *morrisoni, jeanneli,* and *stricticollis* of group *eremita.* One would have to postulate that at the time of dispersal environmental conditions between the localities at which related but isolated forms are now found were in general, or along specific avenues and/or at specific times, within the toleration limits of the species. Such conditions may well have existed, especially in times of Pleistocene glaciation when climates in this area were considerably cooler than at present.

A third possibility, of course, is that dispersal was along ancient river valleys. In areas where modern drainage follows patterns already established at the time of dispersal, closely related forms of *Pseudanophthalmus* would

be endemic to this drainage system. In areas where modern drainage patterns have been established subsequent to dispersal, relatedness of *Pseudanophthalmus* species need not be correlated with the drainage system. The marked change in drainage pattern of southern Indiana resulting from glaciation might be of considerable importance in accounting for unusual distributions of *Pseudanophthalmus* in that area. It would seem of special value in accounting for the presence on the Indiana and Kentucky sides of the Ohio River respectively of closely related *bloomi* and *barberi*. Prior to Pleistocene glaciation a major stream, the Teays, flowed from east to west through central Indiana; its headwaters were probably in the Piedmont of North Carolina and it emptied into the Mississippi basin (Wayne, 1952; Janssen, 1953). At this time the Ohio River was a relatively insignificant stream, probably with its headwaters near Madison, Indiana (Wayne, 1952), more likely an avenue of dispersal than a barrier to distribution as it now seems to be because of its large size. In early glacial times, probably during either the Nebraskan or Kansan glaciation (Wayne, 1952 and personal communication) the Teays system was deranged. This derangement consisted of the separation of the downstream portion of the river, the Mahomet (Horberg, 1950) of Indiana and Illinois, from the upstream portion. The upper portion of the Teays was diverted over a divide into the Ohio Valley, resulting in an enlarged and actively eroding Ohio River following essentially its present course. It seems likely that *barberi* and *bloomi* have been separated at least since that time; *bloomi* on the Indiana side of the Ohio is most closely related to *barberi* from Kentucky, less closely related as recognized by genital characters to the other species of group *eremita* which are found in Indiana (Plates 1 and 2).

The details of preglacial drainage of southern Indiana are not completely known, but there is little suggestion from what is known (Wayne, 1952 and unpublished data) that the localities in which are found species of group *shilohensis* or *stricticollis*, *jeanneli*, and *morrisoni* of group *eremita* were closely interconnected by preglacial streams. Similarly, data available on glacial drainage of Indiana (Leverett and Taylor, 1915; Thornbury, 1950; Wayne, 1952) fail to suggest possible stream connections between these localities. Thus if dispersal of these particular species of group *eremita* and the species of group *shilohensis* was along stream valleys it seems that it must have been along streams existing prior to but not during the erosional cycle (Parker) which began with late Tertiary (late Pliocene) rejuvenation and was complicated by glaciation (Wayne, 1952). However, Malott (1952) presents data which indicate that the Lost River caverns, of which Elrod's Cave the type locality of *jeanneli* is a part, was formed during the Parker erosional cycle; the surface dry bed of Lost River, whose waters are now carried in the underground portion of this river, is entrenched in a Tertiary erosion surface (Lexington peneplain); there is a possibility, however, that these caverns had been formed during earlier erosional cycles and were not occupied by Lost River until this time. These various arguments, admittedly tenuous, would favor the suggestion that *jeanneli* was dispersed across the divide separating the drainage system along which it lies from adjacent ones. They would also suggest that *jeanneli*, which is very closely related to both *morrisoni* and *stricticollis*, less closely related to the other species of group

eremita (Plates 1 and 2), has possibly existed as an isolated species at most since the late Pliocene.

It thus seems that both dispersal overland across divides and dispersal along ancient stream valleys are of value in accounting for certain distributions of *Pseudanophthalmus*. Certainly the two methods are not mutually exclusive. Of considerable interest are the suggestions concerning the possible time of isolation of closely related species: a) two very closely related species of group *eremita*, *bloomi* and *barberi*, seem to have been separated at least since the Kansan glaciation; b) the cave in which is found another species of the same group, *jeanneli* which is very closely related to *morrisoni* and *stricticollis*, may not have been formed until late Pliocene times. Thus there is suggested a maximum and minimum time of isolation of forms that differ from their nearest relative to about the same extent: the maximum since the late Pliocene, the minimum since the Kansan glaciation.

EVOLUTIONARY PROBLEMS AND IMPLICATIONS

The origin of the cavernicolous carabid fauna of North America is still a problem. There seem, however, to be two distinct evolutionary lines represented. The first of these appears to be in what Jeannel (1928) calls the phyletic series of *Trechoblemus*. It comprises the genera *Pseudanophthalmus*, *Neaphaenops*, *Nelsonites*, and *Darlingtonea* (Valentine, 1952). *Trechoblemus* comprises two species, *T. micros* Herbst of Europe and western Asia and *T. postilenatus* Bates of Japan, eyed lucicoles with wings capable of flight, but depigmented. Elongate sensory bristles of the European species suggest preadaptation to cave life, and in the southern part of its range it tends to invade caverns. There is little doubt that the four species of *Duvaliopsis*, eyeless, depigmented cavernicoles endogenous to the Carpathian and Transylvanian Alps are derived from *Trechoblemus* or a form close to it. Whether *Trechoblemus* is the parental stock of this line of North American anophthalmids, and if so how it was dispersed to this continent, are still moot questions. The fact, however, that an epigaean form which might serve as the parent stock of American anophthalmids is not yet known from North America, would seem to argue for a common ancestry for this diverse fauna. For if there were a diverse ancestry there would more likely be remnants of the epigaean ancestors.

A second line has been described more recently by Valentine (1952). It comprises the genus *Ameroduvalius*, in which but two forms have been discovered. There is hardly any question but that it represents a distinct line, probably from the phyletic series of *Duvalius* which otherwise is Palearctic in distribution.

The Palearctic trechine fauna is much more extensive (at least better known) than the Nearctic. In the Palearctic region there are many facultative cave dwellers and true cavernicoles whose epigaean stock is rather definitely determinable. Such cave dwellers range in appearance from those which are heavily pigmented and have fully developed eyes and wings to those which, like our North American species, lack pigmentation, eyes, and wings. Such regressive evolution is characteristic of many cave animals, and various hypotheses have been proposed to account for it (cf. Packard, 1886; Eigen-

mann, 1909; Hubbs, 1938). The hypothesis most consonant with modern genetic and evolutionary interpretations and which is applicable to all regressive phenomena is that formulated by Emerson (Allee *et al.*, 1949). Inasmuch as most characters of an organism are determined by gene complexes, many of these genes having pleiotropic effects, positive selection of random mutations determining characteristics adaptive in a given environment may, since most mutations are deleterious, result secondarily in degeneration of neutral or less valuable characteristics.

Specifically in the cave environment there would seem to be selection for structures and behavior patterns compensating for the ineffectiveness of the eyes. Positive selection for functional qualities might well disrupt balanced complexes of genes for eyes, wings, and pigmentation, which are ordinarily maintained by selection in epigaean environments, but for which there is no positive selection in the cave environment. Casual observations by the author suggest such compensatory adaptations, both structural and behavioral, worthy of further investigation. Elongate antennae and numerous elongate bristles scattered over the body suggest the importance of non-visual senses to these organisms. When captured in an aspirator the beetles soon crawl into the space between the cork and the glass tube; when disturbed in their normal environment they seek shelter in tiny crevices. They persist in clinging to a solid object, so that they will remain on the cork of the aspirator after it has been removed.

One of the most significant features to be noted as one considers these anophthalmid populations is the fact that each is strictly isolated from the others. Yet the cave environment—absence of light, high relative humidity, constant temperature throughout the year—is remarkably similar. Thus this would seem to be an ideal situation for assessing the effect of isolation as an important factor affecting genetic fixation and divergence between populations.

The breeding structure of a population deployed in a linear fashion as along a stream, such as has been proposed for the dispersal of *Pseudanophthalmus* in many cases, is such as to permit moderately rapid fixation of distinctive gene patterns (Wright, 1946). Fixation is even more rapid as units of such a population become completely isolated. Both close inbreeding and the effects of small population size contribute to fixation in these cases.

Gene patterns so fixed may well be ecologically non-adaptive in nature; selection for internal balance, intraspecific or interspecific population adjustments, however, may still be operating so that all adaptive divergence is not ruled out. Genetically determined character differences may be either qualitative or quantitative. Most of the criteria used in recognizing the various species of *Pseudanophthalmus* described above are quantitative in nature, yet there seems to be a difference constant and recognizable enough to separate them. Between others, especially between what have been described as groups, however, there are qualitative differences, particularly in aedeagal characters.

Jeannel and Valentine have followed the practice of recognizing those forms as subspecies which differ from one another quantitatively, those as species which differ qualitatively. This is consistent with their (Valentine, 1943) distinction between raciation and speciation. The former is considered the accumulation in isolation of minor morphological differences, which only

under unusual conditions, such as unusually long isolation, results in qualitative divergence and intrinsically determined isolating mechanisms. Speciation in contrast is considered as a fundamentally psychophysiological phenomenon bringing about separation between organisms living in close geographic and ecological proximity, resulting in qualitative distinctions between populations. Admittedly difficult is the problem of distinguishing between quantitative and qualitative differences, especially in incipient stages of speciation.

When describing divergent populations, it seems more desirable to this author for both practical and theoretical reasons to use the criterion of reproductive isolation, whether extrinsically or intrinsically determined, advocated by Emerson (1945). Practically, it is more readily established whether there is exchange of genes between two populations than whether there could be exchange between them. Theoretically, concomitant with fixation in reproductively isolated populations of distinctive gene patterns resulting in distinguishable quantitative or qualitative differences, there is likely to be fixation, in the absence of positive selection for interfertility, of gene patterns resulting in intersterility. Thus extrinsically determined isolation may in time result in intrinsically determined isolation. This view of the development of intersterility (regression of interfertility) was discussed theoretically by Muller (1942). It has been supported by experiments of Moore (1950) with *Rana pipiens* in which it has been demonstrated that forms found in northern and southern latitudes have developed marked racial incompatibilities together with physiological adjustments of developmental stages to temperature conditions. In forms more widely separated geographically, however, but developing under more similar temperature conditions because of altitudinal differences, only minor incompatibilities have developed. This theoretical concept, as discussed above, has been broadened in scope by Emerson (Allee *et al.*, 1949) to include all regressive evolution.

Germane to this discussion, and significant in its own right, is the fact that there are a number of cases known in which two or three anophthalmid species live together in a single cave. In some of these cases it is most probable, as Valentine (1945) has pointed out, that the populations have been brought together by cave fusion or stream piracy. But other cases are cited by Valentine (cf. esp. 1943, 1945) as suggesting that speciation is an intrapopulational process resulting in qualitative divergence. It is the present author's opinion that the situation with regard to divergence of two populations which are or have become sympatric is better expressed as follows. Should the two populations be compatible, the populations would merge to form a single population. Should the two populations be such that interbreeding results in imbalance, there would be positive selection for mutations tending to further separate the populations, that is for intersterility. Such selection would increase the rate and degree of divergence over that occurring by random fixation.

It must be noted that in the known cases of co-existence, aside from those almost surely brought together by cave fusion, there are a number of cases in which the sympatric species have relatives differing from them in only quantitative respects. According to the views relative to increase of divergence discussed above, it would be necessary to postulate that in each one of these cases qualitative divergence had occurred in that cave in which two or more

forms exist, and that one or more of the forms had subsequently dispersed and given rise to races. It would appear just as likely that populations which had already become qualitatively distinct, having relatives differing from them only quantitatively, have subsequently been brough together.

The fact that two closely related species do co-exist is of considerable ecological and evolutionary significance. On the basis of both laboratory (Park, Gregg, and Lutherman, 1941) and field (Lack, 1944, 1945, 1946) analyses and amplifications of Gause's principle (Gause, 1934), one would suspect that there exists between the co-existing populations some microecological differences. As a whole little is known concerning what if any such differences exist, though Valentine (1952) suggests a distinct microhabitat preference between the genera *Darlingtonea* and *Ameroduvalius* co-existing in caves in the vicinity of Somerset, Kentucky.

SUMMARY

Twelve species of cave carabids of genus *Pseudanophthalmus* from caves of southern Indiana and Kentucky are described. Four species, *eremita, stricticollis, morrisoni,* and *barberi,* belonging to group *eremita,* have been previously described. Eight are new species, representing four distinct groups: *jeanneli* and *bloomi* of group *eremita; youngi* and *donaldsoni* of group *youngi; emersoni* of group *emersoni; shilohensis, mayfieldensis,* and *boonensis* of group *shilohensis. P. morrisoni* and *donaldsoni* inhabit the same cave complex; each of the other species alone inhabits a cave or possibly interconnected caves.

Arguments from relationships suggest that these cavernicoles have been dispersed along ancient stream valleys or overland across divides. There is a suggestion from the data that one form has been isolated at most since the late Pliocene, another at least since the time of the Kansan glaciation.

It appears that *Pseudanophthalmus* represents a single line of descent from an epigaean ancestor. In the cave environment eyes, pigmentation, and wings have been lost. Factors possibly accounting for such regressive evolution are discussed.

The forms described exist as populations isolated in a strikingly uniform cave environment. This represents an ideal situation for assessing the role of isolation as a factor in speciation. Recognizable morphological differences between populations would appear to result from fixation of distinctive gene patterns; in isolation close inbreeding and the effects of small population size contribute to rapid fixation. Extrinsically determined isolation may in time result in intrinsically determined isolation. Emphasizing the important role that isolation may play in speciation, these morphologically distinct isolated populations are described as species.

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Observations on the Reproductive Habits of Darters (Pisces-Percidae)[1]

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The darters comprise an important group of the temperate freshwater fish fauna of the Atlantic drainage of North America. These fishes make up the subfamily Etheostomatinae in the Percidae and over one half of the almost one hundred species are confined to the Mississippi River drainage. A wide variety of breeding habits is exhibited by this group of fishes. It is the purpose of this paper to present the field and laboratory observations on the reproductive behavior of fourteen species and to relate each to the previously published data.

Adequate reviews of the literature on the biology of these fish have been published (Raney and Lachner, 1939; Fahy, 1954). Except for the comprehensive study of the greenside darter by Fahy (1954) the literature consists of only brief papers on biology and life histories. The information presented here along with data on habitat, sex ratio, migration, territory, sex recognition, and eggs has been treated comparatively by Winn (1955).

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Methods, Nomenclature, and Localities

An outline of the field and laboratory observations on the reproductive behavior of the darters studied is presented in the following section. At the beginning of each description the total number of hours of observation is listed. This consists of continuous periods of one-half hour or more, but does not include many hours of observations made when the fish were inactive or were going through typical behavior already noted many times. In all these instances no deviations from the behavior described below were observed. Unless otherwise stated the various aspects of behavior were observed a minimum of 20 times and in most instances over 100 times. In all situations an effort was made to describe the variation in behavior rather than to emphasize any mode of reaction.

Because of space limitations, only a bare outline of the observations is given. In a few instances additional details can be obtained from previously published life histories. Under each species account, a general statement of

[1] This is part of a dissertation submitted to the University of Michigan in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

breeding habits usually appears first and is then followed by detailed observations.

The generic nomenclature is that used by Bailey (1951), and Bailey (in Bailey and Gosline, 1955) but this does not imply agreement with these allocations. Little data has been presented to substantiate these recent nomenclatorial changes. For the most part meristic and other superficial morphological characters have been used for the delimitation of genera in darters. Until the anatomical traits which reflect the broad ecological and behavioral differences between darters are studied and evaluated it seems unwise to make new generic allocations.

The species treated in this paper are as follows: *Percina caprodes* (Rafinesque); *P.* (*Hadropterus*) *maculata* (Girard); *Etheostoma* (*Poecilichthys*) *caeruleum* Storer; *E.* (*P.*) *spectabile* (Agassiz); *E.* (*Doration*) *saxatile* (Hay) which is a synonym of *E. stigmaeum* (Jordan) (Bailey, Winn, and Smith, 1954); E. (*Poecilichthys*) *exile* (Girard); *E. blennioides* Rafinesque; *E.* (*Microperca*) *microperca* Jordan and Gilbert; *Percina* (*Cottogaster*) *copelandi* (Jordan); *Etheostoma* (*Ulocentra*) sp. an undescribed form from the Barren River, Kentucky and Tennessee; *E.* (*Ulocentra*) sp., an undescribed form from the Green River, Kentucky; *E.* (*Boleosoma*) *nigrum* Rafinesque; *E.* (*Poecilichthys*) *maculatum* Kirtland; and *E.* (*Catonotus*) *flabellare* Rafinesque.

The localities where the major portion of the field observations were made, or where laboratory fish were collected, and their relative abundance are as follows: (The term 'common' means that many individuals were seined whereas 'uncommon' means only a few individuals were captured).

MICHIGAN

DOUGLAS LAKE: Shores of biological station, T. 37 N., R. 3 W., Sec. 27, Cheboygan Co.; shallow water zone of sand and some rocks; some vegetation.—*Percina caprodes,* common; *Etheostoma nigrum,* common; *E. exile,* less common.

INLET, SUGARLOAF LAKE: T. 1 S., R. 3 E., Sec. 32, Washtenaw Co.; 100 meters from mouth to weir used for the study of *Esox lucius* by John Williams of Institute for Fisheries Research; width 8 ft. (2.4 m); raceway; current moderate; bottom sand and mud; banks of solid fibrous roots and soil.—*E. exile,* common; *E. microperca,* common.

WHITMORE LAKE: Town of Whitmore Lake, T. 1 S., R. 6 E., Sec. 5, Washtenaw Co.; area around peninsula on south side of lake; sand and emergent vegetation areas of littoral zone.—*E. exile,* common; *E. microperca,* common.

OUTLET, PORTAGE LAKE: T. 1 S., R. 4 E., Sec. 1, Washtenaw Co.; 100-meter stretch of stream from Portage Lake to its entrance into the Huron R.; there are two such outlets and most of the observations were made on the southern-most one; width about 40 ft. (12 m); pools and rapids; current fast; bottom gravel, sand and some rubble.—*Percina caprodes,* common; *E. caeruleum,* common; *Percina maculata,* less common; *E. blennioides,* uncommon.

MILL CREEK: Below dam in Dexter, tributary to Huron River, T. 2 S. and T. 1 S., R. 5 E., Secs. 6 and 31, Washtenaw Co.; width about 40 ft. (12 m); pools and rapids; current fast; bottom gravel and rubble.—*E. blennioides,* common; *E. caeruleum,* common; *E. flabellare,* uncommon.

FLEMING CREEK: 1.25 mi. northeast of Dixboro, tributary to Huron River, T. 2 S., R. 7 E., Sec. 8, Washtenaw Co.; width 10 to 15 ft. (3 to 4.6 m); riffles, raceways, and pools by bridge; current fast; bottom gravel.—*E. caeruleum,* common; *E. nigrum,* uncommon.

TRIBUTARY TO SALINE RIVER: State hwy. 11 crossing, T. 4 S., R. 5 E., Sec. 4, Washtenaw Co.; width 3 to 12 ft. (0.9 to 3.6 m); one half mile series of riffles, raceways, and pools; current fast to slow; bottom gravel, rubble and silt.—*E. caeruleum,*

common; *E. spectabile*, common; *E. blennioides*, common; *E. flabellare*, common; *E. microperca*, common; *E. nigrum*, common; *E. exile*, uncommon.

SALINE RIVER: Section above bridge 0.25 mi. east of above locality with same characteristics except stream 10 to 25 ft. (3 to 7.6 m) wide; same species.

SALINE RIVER: Below park at Saline, T. 4 S., R. 5 E., Sec. 1, Washtenaw Co.; width 20 to 30 ft. (6.1 to 9.2 m); section one quarter mile of rapids and pools; current fast to moderate; bottom mostly rubble, some gravel.—*E. caeruleum*, common; *E. blennioides*, common; *E. flabellare*, common.

ROUSE DRAIN: T. 3 S., R. 5 E., Sec. 13, tributary to Saline River, Washtenaw Co.; width 2 to 10 ft. (0.6 to 3 m); 1 mile series of riffles, raceways and pools; intermittent stream; current slow to moderate; bottom sand and gravel.—*E. spectabile*, common.

BEER CREEK: Section of stream before splitting into Center and Beer Creeks at U. S. hwy. 23, tributary to Raisin River, T. 5 S., R. 6 E., Secs. 25 and 26, Monroe Co.; width 2 to 12 ft. (0.6 to 3.6 m); 0.25 miles of riffles, raceways and pools; intermittent stream; current slow to moderate; bottom sand, gravel and some rocks.—*E. spectabile*, common; *E. nigrum*, common; *Percina maculata*, uncommon; *E. caeruleum*, uncommon.

TENNESSEE

TRACE CREEK: At Hermitage Springs, State hwy. 52, tributary to Barren R., Clay Co.; width 20 to 40 ft. (6.1 to 12.2 m); riffles, raceways and pools; current slow to fast; bottom mostly gravel, some rubble and limestone bedrock.—*E. saxatile*, common; *Etheostoma* (*Ulocentra*) sp. (Barren R. form), common; *E. flabellare*, common; *E. caeruleum*, common; *E. spectabile*, uncommon; and other darters not considered here.

KENTUCKY

EAST FORK OF BARREN RIVER: 5 mi. NW of Tompkinsville on hwy. 63, Monroe Co.; width 30 to 60 ft. (9.1 to 18.3 m); riffles, raceways and pools; current slow to fast; bottom gravel, limestone bedrock and a few larger stones.—*E. saxatile*, common; *E. blennioides*, common; *E. spectabile*, uncommon; *E. caeruleum*, common; *E. flabellare*, uncommon; and other darters not considered here.

SOUTH FORK NOLIN RIVER: At Buffalo, tributary to Green R., La Rue Co.; width 10 to 40 ft. (3 to 12.2 m); riffles, raceways and pools; current slow to fast; bottom mostly gravel and some rubble.—*Etheostoma* (*Ulocentra*) sp. (Green R. form), common; *E. saxatile;* uncommon; *E. blennioides*, uncommon; *E. caeruleum*, common; and *E. flabellare*, uncommon.

Species Observations

PERCINA CAPRODES (Logperch)

Field observations (8 hrs.).—Reighard's (1913) short account of the behavior of *P. caprodes* in Douglas Lake is essentially verified and expanded by my observations in the same lake. The population remains in deeper water until the latter part of June, at which time it migrates to the shallow shoals of fine sand. It is suspected that most of the males migrate shoreward slightly ahead of the females.

On the sand shoals, in 10 to 200 cm of water (4 to 12 inches in Reighard's observations), a few to several hundred males form compact schools or looser aggregations in which there may be one to several females. In general, the females remain outside of the male schools until ready to spawn, at which time a female swims through the school of males and out again. She is followed by a few, or more frequently, many males. When she stops on the bottom one male mounts her back, with his pelvic fins placed ahead of the female's relaxed first dorsal and with his caudal region bent down alongside the female's caudal fin. (Illustrations of these positions were given by Winn, 1955). Both sexes then vibrate vigorously so that they become well buried in the sand, at which time the eggs are laid and fertilized.

A cloud of sand forms above the vibrating pair. Sometimes the female starts to vibrate into the sand before the male mounts. When the females finish egg-laying they swim out to deeper water until ready to spawn again. It appears that at least 10 to 20 eggs are laid at each spawning. One female spawns many times with many males.

The schools consisted of over 100 males and several females. The male school, sometimes as a body, followed one female; usually only a few pursued her. Thus there was a large school of fish in close contact, from which small groups of males occasionally broke away only to rejoin the main body after spawning was completed. Toward the latter part of July the male schools gradually diminished until none were left on the spawning grounds.

The closest male usually mounted the female in typical fashion. Frequently the one or two additional males placed themselves on the sides of the spawning pair and also vibrated. Once an extra male was noted on top of the mounted male and he vibrated simultaneously with the pair. Other odd positions were assumed by these accessory males. The remaining males that could not join the spawning pair ate any eggs that were not well buried. Other males approached the spawning group after the pair started to vibrate. A finger placed under the sand and moved rapidly attracted males to the moving sand.

Very frequently males chased after and mounted other males that swam away from the group and stopped on the bottom, but no vibration occurred. The male underneath either waited for the male on top to swim away or else swam away himself, thereby upsetting the male on top.

When frightened by an observer, the school moved for a short time into deeper water and swam slowly back to their original shallow breeding grounds. Birds flying over the school caused it to spread out and then it resumed its movements back and forth over an area 30 meters long and parallel to the shoreline. Another group spawned under a boathouse in water that was about 1 to 2 meters deep over a sand area roughly 7 by 12 meters. The fish spawned from early morning to early evening, but at night quietly remained on the bottom. In no instance was any pugnaciousness between males observed in the Douglas Lake population.

Percina caprodes breeds in large numbers in the outlet from Portage Lake to the Huron River. In part of this short stretch the bottom is strewn with boulders and gravel and the current is fast. The males maintain themselves over this area, whereas the females concentrate at the base of the raceway-riffle in a pool-like area. The smaller males tend to stay on the sides of the raceway away from the main mass of larger spawning males. When ready to breed a female moves up over the rapids where many males pursue her. After a dash over the rapids, frequently interrupted by spawning, she moves back down the rapids to a male-free area until ready to repeat the process. Infrequently she enters the pool above for a short while.

A male followed a female up the riffle until he spawned with her or lost contact. When she stopped on the gravel, he mounted her and they vibrated vigorously. The vibrations buried them in the fine to moderate gravel, when the eggs were extruded and fertilized. The male-on-female position was the same as described for the lake population.

Frequently a male following a female was approached by another male,

or less often, by two or three males. The attendant male made short dashes of a few centimeters at these intruders or other nearby males, who usually left as a result of these movements. The male then continued to follow the female. Not infrequently, however, while the male was dashing at an intruder, the female would move farther up the riffle where another male took up the chase.

In one case, several male *P. caprodes* were observed chasing one female *P. maculata*. The ratio of *P. caprodes* to *P. maculata* was at least 20 to 1. The latter species bred only on the edge of the pool near the head of the riffle, whereas *P. caprodes* spawned up to this area.

Laboratory observations.—No reproductive activities were exhibited when ripe males and females were placed in 91 by 46 by 37 cm deep aquaria or in troughs twice that size.

PERCINA (HADROPTERUS) MACULATA (Blackside Darter)

Field and laboratory observations.—W. P. Petravicz (1938) made extensive observations in which he noted that the spawning activities are alike in nature and in aquaria. This species spawned in about 30 cm of water and I observed several mating at a depth of 60 cm or more in pool or raceway-like areas (the only time field observations were made).

The fish migrate upstream to their breeding grounds in March or April. They were first observed in the outlet of Portage Lake the last of April, 1953. Once on the breeding grounds, the behavior is very similar to that described for *P. caprodes* in a stream.

The anal and caudal fins, according to Petravicz, are on opposite sides of the female's caudal peduncle. Although I was unable to check the spawning position, it seems likely that the anal and caudal fins of the male are on the same side of the female's caudal region. This position is maintained by the other darters studied; moreover, in the attitude described by Petravicz, the urogenital openings appear to be too far apart for adequate fertilization of the eggs. The male undergoes a striking change in color pattern during the spawning act. Petravicz stated that the females become spent in 2.5 days; this was probably a laboratory observation and does not take place in the field. The rapid laying of eggs occurs in the other gravel burying species when placed under the usual laboratory conditions which are not ideal.

ETHEOSTOMA CAERULEUM (Rainbow Darter)

Field observations (10 hrs.).—Cora Reeves (1907) published a detailed paper on the reproductive habits of *E. caeruleum*, which unfortunately involved two species, *E. caeruleum* and *E. spectabile* (Trautman, 1930). Since it is difficult to sort Reeves' observations, a resumé of observations on *E. caeruleum* is reported here. The study was made on a tributary to the Saline River, at Fleming Creek and at Mill Creek.

The males usually migrate to the breeding riffles in late March. They breed in water from 10 to 60 cm deep, but more often in 25 to 35 cm. The females spend most of their time in the pools at the base of the riffles. When a female swims up onto the riffle, she is immediately followed by one to several males. When she enters an area occupied by a large male, two

or more years old, he follows her and defends an area around her. This is designated a moving territory. The males follow females for a distance ranging from a few centimeters to two or more meters, commonly 0.5 to 1.5 meters. The chase may be terminated before spawning is achieved by the advent of a larger male, or the female may return to the base of the riffle. During the progress of the pair over the riffle, the male actively attempts to keep other males away by making short dashes with his fins stiffly erect. If the interloper does not retreat, the guarding male moves sideways towards him. Sometimes two males move upstream 2 to 3 meters beside each other with fins erect. In this case, both of the males lose contact with the female. The males of *E. caeruleum* appear to fight only with males of the same species. Other details of combat between males can be found in Reeves' article. When not defending his territory, the male sometimes rests his head on the female's back or caudal peduncle.

The males of this species were so abundant in Fleming Creek that they were within 15 to 20 cm of each other. They were spread over the riffle, maintaining temporary mobile territories against intruders. Reeves (1907) emphasized the holdings of the males, but also gave much evidence of the movement of these holdings. My observations show that these holdings become completely shuffled throughout a day. Part of her observations concerned males near large rocks, which enabled the males to identify an area. My observations were made over fine gravel where there was no identifying object for a stationary territory except in a few special cases. Males protected small depressions in the gravel for a longer time than other more uniform areas. They engaged in "sham" battles on the riffles before a female arrived, but a male did not fight in one spot. It is not known if males shift from one riffle to another during the breeding season, although it is doubtful that they do so after the first few weeks of sham battles.

The female is closely followed by the male until she wiggles into the gravel. When ready to spawn, the female forces her head into the gravel while in an almost vertical position, and then moves down and forward so that the ventral half of her body is buried. The male then immediately mounts her, with his pelvics placed on her back ahead of her relaxed dorsal fins, with his pectorals fanned out or moved for balance, and his caudal region bent down beside the anal fin of his partner. Thus they are momentarily in a firm position with the urogenital openings near each other. The two then vibrate rapidly for a moment and the eggs are released, fertilized and buried in the gravel. The female may then move forward on the riffle and spawn one to several times with the same male or several more times with another male. She prevents further egg-laying by swimming into the pool below the riffle, or infrequently into the pool above. Often the females make short sojourns from the pools over the riffles occupied by males without spawning.

The less brilliantly colored yearling males, which are mature in the sense that they have ripe active spermatozoa, have moving territories at times but exhibit little spawning success against larger males. From 1 to 5 or 6 yearling males often chase after large females and usually do not bother to fight each other. Sometimes several yearlings will vibrate at the side of a larger male and female which are spawning. The larger males usually make

no attempt to fight the yearlings unless they try to mount the female, and the large females usually ignore the attempted mountings by the yearlings.

Etheostoma caeruleum ate eggs found in the nests of *Campostoma anomalum, Semotilus atromaculatus* and *Lampetra lamottei.*

Laboratory observations (15 hrs.).—In general the laboratory and field observations agreed. However, it was not possible to study the pool-riffle relationship in aquaria.

Successful spawning occurred in about every third aquarium. When 2 to 5 individuals of each sex were placed in a tank with a gravel bottom (50 by 30 by ± 30 cm deep) one male always became dominant over the whole aquarium. In most instances, the largest reproductively active male was dominant. In 11 of 15 cases an intermediate-sized male was dominant, the larger ones exhibiting no interest in breeding. If a dominant intermediate-sized male was challenged by a larger male, the larger fish usually became dominant in the tank, but this typically required several challenges.

The dominance of a male in a tank in no way prevented the other males and females from eating eggs. The male defended the female instead of any particular area.

Males and females taken from fast water with large rocks seemed less inclined to breed than those taken from fine gravel riffles. The former are usually very dark blue or almost black.

The reactions between the male and female, following, burying, mounting and the final quivering of the two sexes, were the same in the laboratory as in the field. In the laboratory, the anal and caudal fins of the male were never seen to be on opposite sides of the female's caudal region in a previbratory or vibratory position, as was pictured by Reeves (1907) who made only field observations. Even under the best field conditions, it is very difficult to determine exactly the details of the mounted positions. The number of eggs laid per vibration in the laboratory was 3, 3+, 3+, 4, 5, 6, and 6.

ETHEOSTOMA SPECTABILE (Orangethroat Darter)

Field observations (10.5 hrs.).—The previous account of *E. caeruleum* can be used as a description of the behavior of *E. spectabile.* The details of observation show no difference between the two species in migration, territorial or spawning behavior. There were no observed reactions between the two species in the field.

Although both species are abundant on some riffles and are often close to each other, sham battles were never observed between them. This species breeds in shallower water than *E. caeruleum,* at depths of 10 to 35 cm, or more commonly, in 10 to 20 cm. One of the main differences between the two species is that *E. spectabile* tends to breed more often near the heads of slow riffles whereas *E. caeruleum* breeds near the riffle bases. Thus some of the females of *E. spectabile* come down from the pools to the males' territories on these mixed species riffles. On fine gravel riffles, where only *E. spectabile* is present, the females normally move up from pool-like areas below the riffles.

Deserted gravel depressions of *Campostoma anomalum* were often guarded by males of *E. spectabile* and less commonly by those of *E. caeruleum.* Eggs

were laid in these depressions by both species. Most of the *Campostoma* nests were in the slower current near the head of the fine gravel riffles where *E. spectabile* was more abundant. Males of *E. spectabile* showed a tendency to remain in one place when there was a shallow depression or a large rock, either of which was rare on their breeding riffles.

In general, *E. spectabile* breeds in a slower current and lays its eggs in finer gravel than does *E. caeruleum*.

Laboratory observations (15 hrs.).—Laboratory studies on this species gave the same results as those for *E. caeruleum*.

ETHEOSTOMA SAXATILE (E. STIGMAEUM) (Speckled Darter)

Field observations.—No direct observations were made, but this species was presumably spawning on the gravel riffles and at the gravel heads of rubble riffles in depths of 10 to 40 cm in the East Fork of the Barren R., April 6, 1953. The females contained ripe ovulated eggs at that time.

Laboratory observations (4 hrs.).—The reproductive behavior of individuals brought back from Trace Creek, Tennessee, was very similar to that of *E. caeruleum* and *E. spectabile*. Because of this and their similar reproductive habitat, *E. saxatile* is presumed to have similar breeding habits in the field.

Several males and females started to spawn within one hour after they were placed in aquaria. The female, followed by a large male, stops on the gravel. The male places himself on her back in a position similar to those described for the previous species. Then they vibrate vigorously at which time several eggs are laid and buried in the gravel. The vibrations cause partial burial of the pair in the gravel. The females of this species apparently do not gravel-bury as do those of *E. caeruleum* and *E. spectabile*. Probably an average of four or five eggs is laid at each vibration. In one observation, a male mounted the back of a female and vibrated several times before the female responded. In a few instances, where a female was seemingly stimulated and the male was not, she made a few dashes toward, in front of and around the male as if to evoke a response from him.

Dominance and fighting are similar to that of *E. caeruleum*, although *E. saxatile* seemed to have a slightly stronger tendency to protect a stationary area.

ETHEOSTOMA EXILE (Iowa Darter)

Field observations (8 hrs.).—In late March or early April, this species migrates from the deeper water of Whitmore Lake to the shallow edges of the shore where the males protect stationary areas. The females move in from the deeper water to spawn in a male's territory, move from territory to territory to mate several times, and then return to the deeper water offshore. The spawning act usually occurs under the slightly undercut banks on the compact fibrous root material in a water depth of 10 to 40 cm. The position of the pair is as described for the other species.

Most of the males tend to stay in one place under the bank. Some small males attempt to breed promiscuously and stay in no definite area, whereas other small males and all the larger males maintain territories. The territorial males attack intruding males of their own species and at least twice chased individuals of *E. microperca* which were spawning nearby on plants. A male

usually followed a female only in his area; he kept between the female and intruders, which he chased away by headlong dashes or sideways movements with erect fins. While a male was spawning with a female, other males were able to approach the pair without being chased.

Males were never seen in the muddy areas about aquatic plants, where *E. microperca* was abundant. It is difficult to obtain detailed information and usually impossible to see the mating act under the banks. Rarely, eggs are laid only on sand or on roots and organic material on sand, particularly when undercut banks are not available.

Other observations were made in a section of the stream flowing into Sugarloaf Lake, from the inlet up to a weir set about 100 meters from the Lake. The weir blocked *E. exile* from migrating farther upstream and thus was an abnormal situation. Many hundreds of these darters were crowded into this small section of the stream. The males and the females were ripe. No male territorial behavior was observed here. The males mounted males and females over the sand and the fibrous root bank material. A male mounted by another male either sat still until the one on top moved away or else dashed away, thereby upsetting the mounted male. The females upset the males which tried to mount them in the middle of the stream. Frequently a female swam upstream with several males chasing her. Once in a while a female preceded a male under a bank where it was assumed that they spawned on the fibrous root material. Twice spawning was just barely observable. In the mounted position in the current, the pectoral fins were usually fanned so that the male was pressed down on the female.

On April 18, 1953, when only a few individuals were in the outlet stream of Sugarloaf Lake, certain differences of behavior were noted. One male defended a territory centered around a large rock and frequently chased other males away. Also, many of the females were spent.

Laboratory observations (8 hrs.).—Fish were observed in tanks of 91 by 45 by 30 cm and 49 by 30 by 30 cm deep. Individuals placed in aquaria spawned readily as long as they were not overcrowded (no more than two pairs in the small tank).

The observations in the laboratory were similar to those made in the field. The larger males were usually dominant. Often yearling males tried to mount with a larger male and female. At the completion of the act, the larger male always chased the smaller male away.

In the spawning position the male is on top of the female with his pelvics in front of the female's first dorsal fin and his caudal peduncle curved around so that it is beside the female's caudal region. The anal and caudal fins of the male are on the same side of the female's caudal peduncle.

In one tank with coarse sand, filamentous algae, rocks, *Vallisneria* and masses of intertwined roots, the pair spawned in the roots and in the algae except once, when the eggs were laid on a horizontal blade of *Vallisneria*. In two other tanks the eggs were always laid on a fibrous root material but in another tank half of them were laid on the fibrous root material and half in the gravel. In both cases the females put their heads down and wiggled into the material in a manner which resembled to some extent the gravel-burying of *E. caeruleum*. Usually, however, they merely stop in the place where the eggs are to be laid.

ETHEOSTOMA BLENNIOIDES (Greenside Darter)

Field observations.—A few unsuccessful attempts were made to observe this species in the field. Indirect observation on territory and migration are presented elsewhere.

The eggs were found in nature commonly on a green alga (*Cladophora glomerata*), and a moss (*Fontinalis* sp.), and once on an aquatic flowering plant (*Myriophyllum* sp.). Some sort of migration precedes the breeding period. It is presumed from seining and from laboratory evidence that the females stay below the riffles in pool-like areas until ready to spawn. Then they move up through the males' territories to spawn in the usual darter position after which they return to the pools or areas in the riffle without males until ready to spawn again.

In his one field observation, Fahy (1954) stated that some males chased and tried to mount a female over bedrock. They may have been accessory males, because the males on the rubble breeding grounds that I studied were distributed individually (see Winn, 1955). However, the bedrock area may necessitate a different type of behavior.

Laboratory observations (12.75 hrs.).—The observations were made in aquaria 91 by 46 by 37 cm deep, which usually contained two males and two females. The fish were taken from water of 10° to 16° C and acclimatized for 24 hours to 18° to 23° C. Except under unusual experimental conditions, a territory is established and the first eggs are laid in 12 to 48 hours. Discrepancies between Fahy's (1954) and my observations are discussed later.

Soon after introduction into the tank the larger of two males started to follow the female and he became dominant over the smaller male. Eventually the female preceded the male onto the alga where she assumed a position that varied from nearly horizontal to almost a 90 degree angle, usually 45 degrees to 60 degrees. In this particular position the male mounted the female in the usual darter manner. The two then vibrated in unison for a moment, at which time several eggs were extruded. In five observations the number of eggs laid was 4, 5, 5, 6, and 7 per vibration. Also, eggs often stuck together in clumps of 2, 3, 4, 5, 6, and 7 in the laboratory and in the field. The male then stayed beside the female for a minute or so and when she moved forward they sometimes spawned again. While on the alga, they spawned from one to five times, commonly once or twice.

When two females are ready to spawn at the same time and are making short dashes over the alga simultaneously, one female moves beside, over and around the female beside her and may even sit on top of her. A female occasionally did this to unresponsive males. Eggs were not released when two females worked over the alga together.

In some situations eggs were released while the female was poised vertically against the slate wall of the tank. At other times the male and the female spawned together in the gravel. In either event, the eggs were immediately eaten by the parents and by any other fish in the tank. Eggs laid in the alga were not eaten, for they were in the male's territory and thus protected. Occasionally the females or non-dominant male ate the eggs in the alga. The uncommon laying of eggs in the gravel usually happened when not enough alga or similar spawning material was placed in the tank.

The larger male was dominant throughout the tank in thirteen experiments with two males and two females. In one case a smaller male was dominant, but within 8 days the larger male assumed the agressive role. The territory was centered around the material used for egg deposition. Thus from laboratory evidence, the territory appeared stationary, but this needs field confirmation.

In several aspects Fahy's (1954) conclusions differ from those described here. He stated that *E. blennioides* is essentially a night spawner. I made over 100 laboratory observations of spawning during the daytime. *E. blennioides* spawned frequently in the early morning, as soon as it became light outside, and also throughout the day. Fahy's conclusion was based on: 1) about five observations at night in hatchery troughs, 2) the state of development of eggs taken in the field in the morning, 3) the fact that the species seemed to feed more actively at night, and 4) that he did not observe them lay eggs during the day. He further stated that this darter is sensitive to even low intensities of light, but the fish I studied, although much more sensitive to movements of the observer than the other darters, spawned in daylight under a 100-watt bulb. Number 2 photographic floodlights stopped most but not all spawning. Furthermore, every time a light was turned on at night this species was found motionless on the bottom with the fins relaxed and the respiratory rate lower than in the daytime. There is evidence that males recognize other males by color (Winn, 1955); this would be impossible at night. Fahy may not have adequately considered the effect of the early hours of the morning, but due to his evidence the whole subject should be studied further.

Fahy also noted a complete lack of territorial behavior. In the experiments discussed above, strong territories were established by a male whenever two pairs were placed in the larger tanks (91 by 46 by 37 cm deep). No territories were set up in tanks 45 by 25 by 25 cm deep or in those 60 by 26 by 35 cm deep. Fahy made observations on one or two nights in a tank 80 by 35 by 18 cm deep with a 10-watt red photo bulb (mazda). For two reasons I consider his observations to be abnormal. First, the tank size was probably not large enough for the development of a territory. Second, the shallow depth (18 cm) of water may have affected the fish adversely so that they only laid eggs when forced to by internal pressure. On the other hand, there was some current in the hatchery troughs used by Fahy and none in my aquaria, other than slight movement created by the air bubbler. The still water did not adversely affect the behavior of the other darters which live in currents. Indirect field evidence for the presence of a territory was given by Winn (1955).

Fahy also stated that 16 to 52 eggs are laid in one spawning act, but the egg counts in my experiments varied from 3 to 15, usually 4 to 7 by the fish of all ages. The spawning vibrations of his fish lasted from 8 to 12 seconds, whereas in my studies they lasted approximately 1 to 3 seconds, with short or long time intervals before eggs were laid again. Each vibration is considered a spawning act even though the male may stay on the female's back for several sets of vibrations, which Fahy may have considered as one act. The discrepancies between Fahy's data and mine can only be resolved after a series of field observations have been made. It may be that their behavior is easily modified under different social and ecological conditions.

ETHEOSTOMA MICROPERCA (Least Darter)

Field observations (1 hr.).—In April, the population migrates from the deeper organic debris zone of Whitmore Lake to the shallow water near the shore. On May 27, 1952, three or four males were active around aquatic vegetation such as algae, *Potamogeton* and other aquatic flowering plants. One male spawned or attempted to spawn with a female when another male approached the spawning pair. The resident male quickly chased him away. A male stayed in the same place and drove off three other males of his own species but not a male of *E. exile* that came near. Another male a meter away did the same thing.

J. J. Petravicz (1936) gave a fairly complete description of the behavior of this species in nature which is summarized as follows. Until ready to spawn, the females remain outside the shallow vegetated zone occupied by the males. Several males then try to assume the spawning position with one female. Finally, after a chase, one male assumes the mating attitude. The pelvics of the mounted male rest on the sides of the female in front of the first dorsal fin (see also laboratory observations). Vibration of the two sexes then takes place. One egg is laid and then a new place is selected to lay another egg. After several are laid, the female goes into deeper water until ready to spawn again. The eggs are laid vertically on plants or other objects, and in the sand. A male will often mount another male.

Laboratory observations (6 hrs.).—Ten individuals about equally divided between males and females were placed in an aquarium 60 by 45 by 30 cm deep, supplied with abundant aquatic plants. The males chased both males and females. When one male was approached by another male, he swam away, whereas a female would remain. She then preceded the male to the branch of a plant where they spawned. Sometimes a male mounted another male which remained motionless for a second and then darted away upsetting the male on top of him, or the bottom male swam away as soon as another male tried to mount. One male, for a period of several days, remained in one small area and dashed at males and females. Otherwise territorial behavior was not recognizable.

The spawning position of the pair was usually vertical, but varied as much as 30 degrees off the vertical in either direction. However, males attempted to spawn with females when resting horizontally on the substrate (sand, gravel, hard mud) and were successful if the females did not have a chance to swim up to a plant frond. The typical sequence of behavior is the same as that observed in the field.

Three males, (one large, two small) and four females were placed in an aquarium 45 by 25 by 20 cm deep. The larger male set up a territory 25 cm in diameter around the *Vallisneria*. He chased the other two males away from this area, which included the space up in the plants as well as at the bottom. He reacted to his mirror image or to another male in the same manner, erecting all but the pectoral fins, and then dashed at the intruder. The two smaller males erected their dorsals at each other when they followed a female in the end of the tank not covered by the large male's territory. Occasionally, when a small male followed a female into the large male's territory, the small male was immediately chased away. The two small males

mounted a female in odd positions up in the plants and the large male tried to vibrate sideways against her, which toppled all four. The large male immediately chased away the two smaller males. In one situation a small male came down on top of the large male but was soon upset. The large male's pugnacious activities tapered off as the females became spent, but this behavior was soon renewed when two ripe females were added. It looked as though he also chased away the spent females that remained in the tank. In this particular aquarium, the males made no mistakes in sex recognition. They spawned quite successfully on several kinds of aquatic plants.

Unfortunately, J. J. Petravicz did not dissociate his field observations from his laboratory observations, although he stated that they were similar. Many of the observations appear to have been made in a 12 gallon aquarium, with many fish rather than a few pairs. He mentioned once that the fish spawned on the bottom sand when only a few plants were present. Our observations are not always in agreement. For example, Petravicz noted no territorial behavior. Placing too many fish in a tank results in abnormal behavior, which may be resorted to only rarely under field conditions. When two pairs are placed together, one male usually establishes a definite territory, and I observed such territories under natural conditions. In aquaria with plenty of vegetation they almost always spawned in a nearly vertical position, as was also observed in the field. A breakdown in sex recognition occurs under crowded laboratory conditions, but was not observed in the field and occurred only rarely in aquaria that contained only two or three pairs. Occasionally, even under uncrowded aquarium conditions, a male will try to mount a male. Yearling males which show less tendency to guard one area are most often mounted by the older males.

In the spawning position, the anal and caudal fins of the male were observed to be on one side of the female rather than on opposite sides of the female's caudal region as Petravicz stated.

PERCINA COPELANDI (Channel Darter)

Field observations (10 hrs.).—The field observations on reproductive behavior were reported by Winn (1953).

The males maintained territories slightly less than a meter in diameter, the center of which contained a large rock. The females came in over the males' territories from the deeper water of the river and spawned promiscuously with the males in the usual horizontal manner. The eggs were thus buried in the gravel.

The males moved out of their territory to feed, and both sexes when alarmed went to deeper water, the males retreating last.

Laboratory observations.—Observations were attempted in aquaria about one half the size of the normal male's territory, but no reproductive activity was detected.

ETHEOSTOMA (ULOCENTRA) sp. (Barren River form)

Field observations (1 hr.).—On April 7, 1953, in Trace Creek, Tennessee, live specimens of this darter were collected and brought to Ann Arbor. At this time some of the females had a few ripe eggs and would presumably

have spawned in about a week. No eggs were found in the field, but large individual males had established widely scattered territories in the pools and raceways. They were found individually under slate rocks 15 to 30 cm in diameter and in depths of 30 to 300 cm. *Etheostoma flabellare* also held areas under separate rocks in the 30-centimeter depths and generally in shallower water. All the males of *E.* (*Ulocentra*) sp. were ripe. The presence of large males under the large rocks indicated a surplus of yearling males without territories.

Several observations were made in Trace Creek on April 28 and 30, 1954, which slightly modified the conclusions from the above observations. At this time the large males (3 years old) were found to defend weakly demarcated territories in the deep pools (50 to 90 cm deep) and deep areas over the limestone bedrock area, both with fairly swift currents. The rocks were free of silt. Apparently last year's observations were of a mass pre-breeding migration, whereas these notes were made in the middle of the reproductive period. Here, the males did not defend the large broken slate rocks whereas *E. flabellare* defended these rocks which had its eggs on the under-surfaces. Smaller males of *Etheostoma* (*Ulocentra*) sp. were found on the heavy gravel and large rock riffles and the shallower (plus 20 cm deep) raceway-like limestone bedrock areas. This species was much more common over the sheets of limestone bedrock than over the large rubble riffles.

A large male in a pool chased several males away and followed after a female in the lower end of the pool. After he came close to her she drifted out of the pool onto the riffle below, as though to keep away from him. He followed her halfway out of the pool, but then returned to the deeper part of the pool where he remained for more than one hour. What apparently was the same individual was observed in the pool the next day. More field observations are needed in order to verify the conclusion, based on laboratory evidence, that this species maintains a stationary territory.

Laboratory observations (8 hrs.).—Two pairs were placed in an aquarium 91 by 46 by 20 cm deep. They were taken from a water temperature of 13° C, acclimatized several days and placed in water of 21° to 22° C. The largest male became dominant throughout the tank. The few times a male followed a female she kept swimming away from him, and in a few cases a male dashed at a female. The females did not spawn but spent most of their time attempting to swim up the sides of the tank. After 24 hours, the water depth was increased to 37 cm and the behavior of both sexes changed markedly. Within one-half hour a male started after a female, who soon laid eggs, and the females no longer attempted to swim up the sides of the tank. Other pairs placed directly into water 37 cm deep spawned within two hours. This illustrates the importance of proper water depth, and is correlated with the depths at which large individuals of this species were found in the field.

In the deeper water, both pairs immediately began to spawn in approximately a vertical position on the slate walls of the tank, on the slate rock which leaned against the wall, and on a large granite rock. All activity was confined to the end of the aquarium where the male maintained his territory. A male followed a female and tried to mount whenever she stopped, but the female swam away before he could get on her back. Then

the female swam up vertically onto the slate rocks, with the male following. The spawning position varied from a 45 degree angle to a slightly obtuse angle. The male placed himself on the female's back with his pelvics in front of her relaxed first dorsal and with his caudal and anal fins curved to one side of her caudal peduncle. The pectoral fins were used for balance. The pair vibrated vigorously and one egg was emitted which adhered to the rock. Quite often the female laid several single eggs as the pair ascended the side of the rock. Eggs were laid from the base of the rock or slate wall to as much as 30 cm off the bottom.

In six instances of simultaneous introduction into tanks, the larger male was dominant over the smaller male, and at no time was this relationship reversed. The dominant male tended to stay in about two thirds of the tank, where the female remained most of the time and laid her eggs. The dominant male followed either female all over the tank and would chase the inferior male whenever encountered. Occasionally the smaller male spawned with the unoccupied female. If the larger male followed a female away from where eggs had been laid, the smaller male quickly devoured them. The tank size must have been approximately equal to or slightly smaller than the male's normal territory. These activities are presumed to indicate a stationary territory, but only field observations can verify this.

In another experiment, two small males were placed in a tank and the larger one became dominant. Later a still larger male was introduced and the intermediate male remained dominant for seven hours, until the largest male challenged him. Even though the largest male was now dominant, the small male still was more agressive than if they had been introduced together.

Fighting technique was much the same as in the other darters, with each male faced in opposite directions and with their fins elevated and stiff. After dominance was established, the male merely dashed with fins erect at his weaker adversary who swam hurriedly away with fins depressed. The male often briefly elevated his fins at the approach of a female and in a few instances chased her if she happened to be in his path when he was attacking a male.

Not only does the inferior male eat eggs, but a female that is not being pursued will also devour some of the eggs. Normally, in the field she would not be in the spawning territory unless ready to lay eggs.

ETHEOSTOMA (ULOCENTRA) sp. (Green River form)

Field observations.—This species was found in the pools and in deeper raceways with large rocks. In a collection made on April 8, 1953, from the South Fork of the Nolin River, all males were ripe and some females had a few ripe eggs, indicating that they would spawn in about a week.

Laboratory observations (7 hrs.).—No differences in reproductive behavior were noted between this species and the Barren River form, although they are distinguishable morphologically. This fish is slightly smaller than the one from Barren River.

A female of this species was placed in a tank with two males and two females of the Barren River form. The larger male readily spawned with her as did the inferior male when the dominant male was occupied with another female. A male Green River specimen was introduced into an

aquarium with two pairs of the Barren River form. The larger male of the Barren River form remained dominant and the small male tried to spawn with the females when chance afforded. Eggs of the Green River form fertilized by sperm of the Barren River species hatched, but no attempt was made to rear the young.

ETHEOSTOMA NIGRUM (Johnny Darter)

Field observations (1 hr.).—The normal behavior involves an April migration to the spawning grounds. The males arrive slightly before the females, usurp territories, and clean off the underside of the selected rock by upside down movements. The females stay out of the areas occupied by territorial males until ready to spawn. They frequently move through these areas without spawning, as was noted in all other species of darters observed in the field.

A brief observation of the spawning behavior indicates that it is similar to laboratory observations.

The number of eggs found in nests varied from 30 to 1150. Counts varied as follows: 30, 47, 70, 870, 1080, 1100+, and 1150. Small counts are more common near the beginning of the reproductive season. Evidence that the population was saturated to a level controlled by the nesting sites was particularly evident in Honey Creek (3.5 miles northwest of Ann Arbor) during the spring of 1954. Here, a few males were guarding some eggs on the underside of fibrous clay pieces of sod that had broken loose from the bank. These peripheral sites, compared to the normal rock nests, were quite unsatisfactory because the eggs did not adhere satisfactorily and many had dropped off. Also, many of the remaining loose eggs were covered with fungus. Atz (1940) listed many objects upon which eggs are laid but he did not include the above type of material.

Laboratory observations (15 hrs.).—Atz (1940) described the behavior of one male and female of *E. nigrum olmstedi* in an aquarium. The following observations on *E. n. nigrum* expand and verify his description.

A typical description of spawning behavior is as follows. Three males and three females were introduced into an aquarium 91 by 46 by 37 cm deep. The males set up territories under the sloping rocks, and in so doing they became much darker. They defended actively their areas against all species except those that are three or four times larger, and these normally could not reach eggs under the rocks. Each dark male spent much time moving upside down under the rock. This cleaned off any attached sediment. This behavior is the same qualitatively whether a male is or is not guarding eggs. The caudal, anal and pelvic fins swept over the rock while the inverted position was maintained by the pectorals. Before any eggs were deposited, the males often made excursions outside their territory but returned within a short time.

Within 24 hours, in the tank with 3 individuals of each sex, the females started to lay eggs with the largest male. The females remained outside the territories until they were ready to spawn a clutch of eggs. When the female approached a male's territory, he frequently came out to meet her. His fins were often erect on her first approach but were immediately relaxed, apparently after recognition. If a male approached, the resident male dashed at

him with his fins erect. The male usually preceded the female under the rock where he immediately started moving upside down over the rock. These movements were made at a faster rate than when a female was not present. If properly stimulated, the female moves in under the rock, turns upside down and the inverted pair move jerkily over the rock beside each other. Tactile contact between them is made with the pectoral fins and sometimes other parts of the body. In another instance eggs were laid while the male was upright, but he soon turned over and moved across the eggs. The female stopped every few seconds or so to press her urogenital papilla against the rock to deposit a single egg. Rarely two or three eggs are laid one immediately after the other. Sometimes the male turned right side up for a few seconds while the female continued to lay eggs, but usually he moved beside her. The eggs were laid on the part of the slanting rock nearest the bottom. The female stopped her upside down egg-laying movements occasionally to pause while on her dorsal fins or she turned upright to rest. The male pushed the female's side with his snout until she turned upside down and if inverted, until she started movements over the underside of the rock. Once, the female left the nest but upon her immediate return, he prodded her sides. The female deposited one clutch of eggs in slightly more than one half hour; then she left the nest. When no females were present, the male continued to rub the eggs, interrupted by brief pauses. When the male turned upright he sat under the rock fanning his pectorals back and forth so that a current of water moved over the eggs. His dorsals also moved back and forth across some of the eggs. In three cases while a large male was spawning with a female, a smaller male came under the rock and moved upside down with them. When the two males turned right side up the small male was vigorously chased away. This behavior suggests that the male continually or intermittently releases sperm when the pair is moving around in the inverted position. In all other darters the only time a male could approach close to a pair was when they performed a mating act. Atz (1940) stated that the female quivered slightly but this was not observed in most cases by me. The few eggs with fungus are eaten by the male. After the eggs were laid the male periodically turned upside down and moved over the eggs. This motion kept them free of silt. Unattended eggs in other tanks were gradually covered by silt particles. The male also fanned his pectorals while in the upright position sending a current of water over the eggs.

In four aquaria the larger of two males received all the eggs from two to three females.

In a tank with one large male guarding eggs and a small male protecting a rock with no eggs, the rocks were transposed. The large male continued to work over the empty rock whereas the small male worked over the eggs under his new rock. After a short period, the larger male only turned upside down 2 and 3 times compared to 6 to 13 times in 5 minutes when the eggs were present. Also, only a very small part of the time was spent in the upside down position. The small male turned upside down 2 and 6 times but spent most of his time rubbing over the eggs; he turned very dark. The large male left his empty rock and went to the small male's rock where the large male was vigorously chased away. Earlier the small male without eggs did not chase the large male. The large male chased a female from

his empty rock. The small male was then removed. The large male went over the rock with eggs but soon returned to the empty rock to fan it with his pectoral fins. He wandered about the tank, although he encountered the eggs several times. One hour after the small male was removed, the rocks were returned to their original positions. The large male did not take care of the eggs even 10 hours later. The eggs had hatched by next morning. These observations indicate that a male defends weakly a rock without eggs, but, when eggs are added, a strong defense of the rock develops. Adams and Hankinson (1928) removed a sheet of tin with eggs from a guarding male and the male returned to the place where the tin and eggs once were.

The evidence indicates strongly that the females of *E. nigrum* lay five to six — usually six — clutches of eggs consisting of 30 to 200 eggs. The following counts of eggs laid with one male, usually within one day, were recorded: 39, 70, 130, 138, and 198 (see also field counts). The larger numbers were laid by larger females. These numbers divided into the total number of eggs in the ovary indicate that commonly, six clutches are laid. The eggs are also distributed in approximately six size groups. Examination of females in the middle and at the end of the reproductive season indicated that all the eggs in the ovary are laid in one season.

In a single instance eggs were scattered over the surface of a rock, suggesting the habits of *Etheostoma* (*Ulocentra*) sp., but they were immediately eaten by the male.

A small male without eggs was given some eggs of *E. blennioides* which he cleaned and guarded until they became infected; then he ate them.

Other observations similar to those described were made in tanks 50 by 30 by 30 cm deep and 91 by 46 by 30 cm deep.

ETHEOSTOMA MACULATUM (Spotted Darter)

Field observations.—The only available information on the reproductive habits of this darter was presented by Raney and Lachner (1939) and is briefly summarized below.

The eggs are laid in several layers in a wedge-shaped mass under stones, rather than in a single layer as in *E. nigrum* and *E. flabellare*. The male guards the eggs in water 15 to 60 cm deep. The minimum distance between nests was 1.2 meters. Whether the male cares for the eggs other than guarding them is not known. Small males without holdings were observed in the vicinity of the nests.

The eggs are laid in batches in an upside-down position probably from two to four times during a single spawning season.

Laboratory observations.—No laboratory studies have been made.

ETHEOSTOMA FLABELLARE (Fantail Darter)

Field observations.—Lake (1936) has made the only observations on spawning in the field. The males set up territories under rocks while the females move upstream into these territories to spawn. They deposit their eggs upside down under a rock and then leave the region of the male's territories. Under the rocks, the substratum usually consists of gravel and the current is negligible and variable.

The eggs are laid in contact in single-layered patches, and Lake (1936) found their number to vary from 8 to 562 with an average of 169. Counts made by the author were 62, 105, 109, 125, 250-300, and 298.

Laboratory observations (12 hrs.).—Only the major elements of the reproductive behavior are presented, because most of my observations merely verify the description given by Lake (1936).

After a migration to the spawning grounds, the males establish territories under rocks. The males then move around under the rock so that the bulb-like tips of the dorsal fins rub the undersurface of the rock and clean off the surface. When a female reaches the periphery of a territory, the male comes out to meet her. She moves forward toward the nesting rock while the male precedes her under it and very rapidly executes circles and figure eights. These movements may well attract the female. Occasionally the female may go underneath the rock first (Lake, 1936). The pair sometimes comes out from under the rock several times before they remain to spawn. The female then turns upside down and, with the male right side up and faced in the opposite direction, they move around in figure eights and circles. In this position the male often nudges her caudal peduncle with his snout, especially if she stops. The pectoral fins touch the sides of the body of each sex and may present contact stimulation. She then stops, presses her vent against the rock above and vibrates slightly, at which time one egg is extruded against the rock to which it adheres. At the precise moment when she starts this maneuver, the male flips over, fertilizes the egg with a brief vibration, and immediately returns to the normal position. The start of the female's vibrations may stimulate the male to fertilize the egg. This behavior proceeds until the female, always upside down, has laid a clutch of 34 eggs on the average (Lake loc. cit.). Then she leaves or is chased away until ready to lay another clutch. When the female is in the normal position after laying eggs, she can only prevent an attack by the male by one or two methods; either she turns upside down again or she leaves the area. Sometimes the male attacks the female if she rests too long under the rock. The pectoral and caudal fins are used for movement while in the nest.

When the male is under the rock alone the swollen bulbous tip of the spinous first dorsal and the soft rays of the second dorsal rub the eggs. Lake (1936) found that without care the eggs became infected. To some extent the pectorals are fanned back and forth with the body in a stationary position, presumably to aerate and clean the eggs.

The rocks have to be exactly the right height from the bottom in order to be chosen for a nest site. This varies from 1.5 to 2.5 cm. More specifically it has to be high enough so that when the female is upside down, resting on her two dorsal fins, her vent is in contact with the rock above or can be pressed against the rock with a slight stiffening of the dorsal spines. The male's dorsals, with the fish in the upright position, have to be in contact with the nest stone. The only possibility of variation in the height of the male is a stiffening and relaxing of the pelvic and anal fins. In one case a female was under a rock that was too high for her ventral side to maintain contact with it. She made a series of quick flips to the upside down position, made contact with the rock above, but immediately fell down, and eventually sought a more suitable spawning site. When two females enter a nest, only one remains to spawn for the other is chased out by the male.

In two instances rocks with eggs were lifted and replaced; all the eggs were eaten within a few hours.

If another darter approached, the male dashed at it but remained partially

under or near the stone. At times the male actually hit the fins or body of his opponent. Other species are attacked by the male as long as they are not too large.

When chasing other males and females or when a female is under a rock, the males darken considerably. Unless temporarily stimulated by fighting, those males guarding eggs are darker than ones without a nest. The head turns jet black and the vertical bars along the side become prominent, black and very conspicuous. The female also darkens slightly when under a rock with a male, but she is never as intensely black as the male.

In six cases in aquaria, females did not spawn on the underside of rocks with the males. Instead they laid eggs one at a time on the slate walls of the aquaria and on a few larger rocks. The eggs were eaten immediately by both sexes. Eight times the number of eggs laid under these abnormal conditions were 1, 1, 1, 1, 1, 2, 3, and 6. Only the single eggs were satisfactorily attached to the walls of the tank. It was assumed in these situations that the space under the rocks was not adequate. At least 10 other times after the introduction of a pair into a tank no spawning occurred.

DISCUSSION

The fourteen species of darters considered exhibit a wide variety of breeding habits. For this reason and because many of these fish can be readily observed in the field and laboratory it is clear that the darters are a valuable group for the study of comparative ecology and behavior. A study of many other species of darters and more detailed investigations of those whose behavior is described here should clarify certain phylogenetic problems. It should also aid in a better understanding of territoriality, sex recognition, bisexual behavior and other activities.

The darters studied here can be grouped generally according to their reproductive habits. *Percina caprodes, P. maculata, P. copelandi, Etheostoma caeruleum, E. spectabile,* and *E. saxatile* all lay their eggs in gravel. They can be placed in minor groups by the fact that the three species of *Percina* do not exhibit the highly evolved fighting behavior between males which is displayed by the males of the three species of *Etheostoma. Etheostoma exile* lays its eggs on banks of fibrous root material or occasionally on sand. The species which lay their eggs on plants (*E. microperca* and *E. blennioides*) are quite divergent in that one utilizes mostly flowering aquatic plants and the other utilizes algae or moss. The two forms of *Etheostoma* (*Ulocentra*) spp. lay their eggs in vertical or near-vertical positions on rocks. In all the above species the male is on top of the female when a pair spawns whereas the male is beside the female when the eggs are laid in an upside down position by *Etheostoma nigrum, E. maculatum* and *E. flabellare* (illustrations of the spawning positions in Winn, 1955). The position has not been observed directly in *E. maculatum. Etheostoma nigrum, E. maculatum,* and *E. flabellare* all lay small masses of eggs on the underside of stones. However, their methods of egg deposition vary. The above variations and many others which do not fall into the above groupings have been discussed in detail by Winn (loc. cit.).

Several factors markedly affected the behavioral response of the darters

in aquaria. The amount and type of substrate is particularly important. Obviously the material used for the deposition of eggs must be proper but also the placement and quantity of such material affects the fishes' behavior. It was not enough to place a little alga on a rock for *E. blennioides* but an amount sufficient to form a large mat was needed for normal egg deposition. Whether the fish will maintain a territory or will spawn at all is often determined by the available space. The critical space requirements necessary for males of *E. blennioides* to establish a territory were described. The dimensions in the horizontal plane seem to be generally the most important. Thus it is necessary to give the dimensions of aquaria in studies of this type and not the capacity in gallons. However, depth is also important. The fact that *Etheostoma* (*Ulocentra*) sp., Barren River, bred in a depth of 37 cm and not in 20 cm of water adequately demonstrates this. The number of individuals placed in a tank is also critical. Too many individuals of *E. microperca* in a small tank results in a complete breakdown of sex recognition. Other examples were described under the species accounts.

Additional factors of importance are light, temperature and water condition. For the most part these were close to those found in the darter's natural environment. Temperatures somewhat above normal did not affect the natural spawning acts but did shorten the breeding time considerably. Fortunately many of the species were observed with ease in streams which made it easier to emulate the proper conditions in the laboratory.

Many of the discrepancies between the observations of other authors and those described here appear to be the direct result of the many factors discussed above. For instance, the observations made by J. Petravicz (1936) appeared to concern many individuals in small tanks, where territories were not established and sex recognition was weak. Under uncrowded conditions this usually does not occur. Because of this great variation due to tank conditions a description of the situation in considerable detail, and even more so than was done in many instances in this study, is extremely important to the comparison and interpretation of results.

Certain variations of behavior were noted in aquaria and less frequently in the field. Manipulation of the substrate, space and the number of individuals was easily accomplished in aquaria. However, in the natural stream a fish like *E. caeruleum* breeds both on fine gravel and in rubble riffles. *Percina caprodes* bred in schools in the one lake population observed but exhibited a simple type of territoriality in a stream population. Territorial expression was easily prevented by overcrowding in some species, e.g., by placing a few pairs of *E. blennioides* in a small tank. *Etheostoma caeruleum* tended to maintain a more stationary territory when large rocks or gravel pits were present than when they were over a uniform fine gravel area. Differences were described in the material upon which *E. exile* laid its eggs under choice and non-choice situations. Sex recognition by males of *E. microperca* and by *E. exile* completely broke down under crowded conditions. It might be said here that less variation in many but not all respects was found in the behavior of *E. nigrum* and *E. flabellare*, the more specialized darters. The above examples and other observations recorded on the darters demonstrate adequately a plasticity of behavior that varies according to the environmental

conditions. This plasticity in the darters is different from the impression one obtains from reading the descriptions of the behavior of the three-spined stickleback and other fishes by the European behaviorists (i.e. Tinbergen, 1951, 1953 and other papers). Much of the behavior, especially its variation, in the darters cannot be described as completely innate but it is the result of a complex interaction between the environment and genetic factors.

SUMMARY

The reproductive behavior in the field and in aquaria was given for fourteen species of darters. The observations were compared with those of previous investigators.

The darters were grouped on one basis into those species which spawn in gravel, on plants, on the side of rocks and on the undersurface of rocks. The male is on top of the female when eggs are laid in all the species except those which lay small masses of eggs on the underside of rocks. Here the male is beside the female.

The effects of the substrate, size of aquaria and the number of individuals on variations of behavior were briefly discussed.

The variation in the expression of territoriality, sex recognition, and other traits was discussed.

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A Study of Dog Carcass Communities in Tennessee, With Special Reference to the Insects[1]

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Many small communities in nature persist for varying periods and ultimately disappear by merger with the larger communities within which they occur. To such units I apply the term microcommunity. The term microsere has been applied by Mohr (1943) to the seral sequence which occurs in small communities of this nature. Microcommunities and microseres are of interest to ecologists in that they are frequently of importance in influencing the structure of the major communities in which they are found.

Many studies of the microcommunities associated with carrion have been published. Early recognition of this particular microcommunity is indicated in Brehm's Thierleben (Taschenberg 1877), which contains several plates depicting insect assemblages at various types of carrion and which gives accounts of the habits of some carrion-frequenting insects. Among later and more detailed studies, mention may be made of those of Mégnin (1894), Johnston & Villeneuve (1897), Motter (1898), Illingworth (1926), Holdaway (1930), Walsh (1931, 1933), Fuller (1934), Kaufmann (1937), Cole (1942) and Howden (1950). Although many of these studies are excellent and thorough, numerous aspects of carrion microcommunities remain uninvestigated. The present paper attempts an analysis of dog-carcass microcommunities with particular reference to seral development, seasonal variation, and environmental factors.

To avoid redundancy, and in the interest of brevity, the terms *community* and *sere* will generally be used in this paper to refer to carcass microcommunities and microseres. The prefix *micro-* will be added when it seems desirable to distinguish these entities from larger communities and their seres.

Acknowledgments.—I wish to express gratitude to Dr. Arthur C. Cole, Jr., for his encouragement, interest, and very helpful suggestions. I am indebted to the many specialists who identified specimens, as follows: Non-insectan arthropods: Clarence J. Goodnight (Phalangiida), Willis J. Gertsch (Araneae), Edward W. Baker (Acarina, excluding Ixodidae), and Harry D. Pratt (Ixodidae). Orthoptera: Fred A. Lawson (Blattidae) and A. B. Gurney (Acrididae and Gryllidae). Hemiptera: R. I. Sailer. Coleoptera: William H. Anderson (adults of Dermestidae, Hydrophilidae, and most larvae of Coleoptera), R. H. Arnett (Silphidae adults), O. L. Cartwright (adults of Scarabaeidae and Trogidae, larvae of Cantharidae and Leiodidae), Edward A. Chapin (Cleridae adults), Lorin R. Gillogly (Nitidulidae adults), Milton W. Sanderson (Staphylinidae adults), and Rupert L. Wenzel (Histeridae adults). Lepidoptera: Hahn W. Capps (Thyrididae adults and all larvae of Lepidoptera), W. D. Field (adults of Papilionidae, Nymphalidae, Hesperiidae, Lycaenidae and Sphingidae), and J. G. Franclemont (adults of Geometridae and Phalaenidae). Diptera: Curtis W. Sabrosky (most adults of Dip-

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tera), H. R. Dodge (certain Sarcophagidae), A. Stone (Scatopsidae), and Willis W. Wirth (adults of various Diptera, and all dipterous larvae). Hymenoptera adults: Arthur C. Cole, Jr. (Formicidae), K. V. Krombein (Apidae, Colletidae, Halictidae, Scoliidae and Vespidae), C. F. W. Muesebeck (Proctotrupidae and Braconidae), L. M. Walkey (Ichneumonidae), and L. H. Weld (Cynipidae). Flowering plants: Judson K. Underwood and Frank W. Woods. Fungi: Lester M. Oswald.

MATERIALS AND METHODS

STUDY AREAS AND CARCASSES

The field study for this research was conducted at a locality about one mile south of the city limits of Knoxville. Official weather records were obtained from the Knoxville Municipal Airport, located a distance of nine miles from the study area. Snow during the period of study never exceeded "traces" according to the records; most of that which fell melted shortly afterward. Normal monthly temperatures and precipitation and deviations from normal during the period of study are shown in fig. 1. The figure shows that temperatures were above normal for every month except November, 1951.

The principal portion of the field work was conducted between May 7, 1951, and May 14, 1952. The carcasses were placed in various wooded and non-wooded areas on and near the University of Tennessee Cherokee Farm.

Under the hypothesis that carcass seres in different habitats would be different, early in the study a tentative selection was made of a variety of areas in which to place carcasses at intervals throughout the period of field work. Nine such areas were originally selected. Some of these areas were later abandoned insofar as placing additional carcasses in them is concerned; however, at least one carcass sere was studied in each of the areas.

Enough areas were used to prevent the necessity of placing a new carcass in an area where other carcasses were located, except carcasses which were in a late stage of decay. Further, each area was large enough to prevent the necessity of placing a new carcass within 50 feet of an old carcass, except for carcasses which were comprised of practically nothing except scattered bones. One reason for such temporal and spatial distribution of carcasses was to prevent excess migration of arthropods from a carcass in one seral stage to a carcass in an earlier or later stage, with subsequent alteration of the normal successional sequence.

Cattle roamed over all the non-wooded areas throughout most of the study. The pastures were grazed from light to medium intensity. It is probable that the presence of cattle and their droppings had an influence on the carrion fauna. The wooded areas were free of domestic animals (except stray cats and dogs). Human visitors were relatively uncommon in any of the areas. The study areas are as follows:

Area 1—mixed mesophytic woodland in a small hill-surrounded basin. The trees were of medium density. Japanese honeysuckle (*Lonicera japonica* Thunb.) was the chief constituent of the rather dense ground cover.

Area 2—a small hill-surrounded basin. The trees were of medium density. The dominant tree species was box-elder (*Acer negundo* L.); other trees were sparsely distributed. Perennial herbs formed a ground cover which was of medium density over most of the basin floor.

Area 3—open pasture with a few scattered medium-sized trees.

Area 4—pasture in which a few large trees were scattered.

Area 5—oak-hickory association near the top of a hill with medium slope. Large trees and large shrubs were present in medium density. Herbaceous growth was sparse. A well-defined layer of leaf litter carpeted the woodland floor.

Area 6—mixed mesophytic woodland on a hillside of medium slope. The trees were distributed with medium density. Japanese honeysuckle was the principal constituent of the rather dense ground cover.

Area 7—scrub-pine (*Pinus virginiana* Mill.) consociation. Both trees and shrubs were fairly thinly scattered. A grass, probably broom-sedge (*Andropogon virginicus* L.), formed a dense ground cover.

Area 8—Carex-Equisetum-Acorus associes in a small marsh. The soil was generally

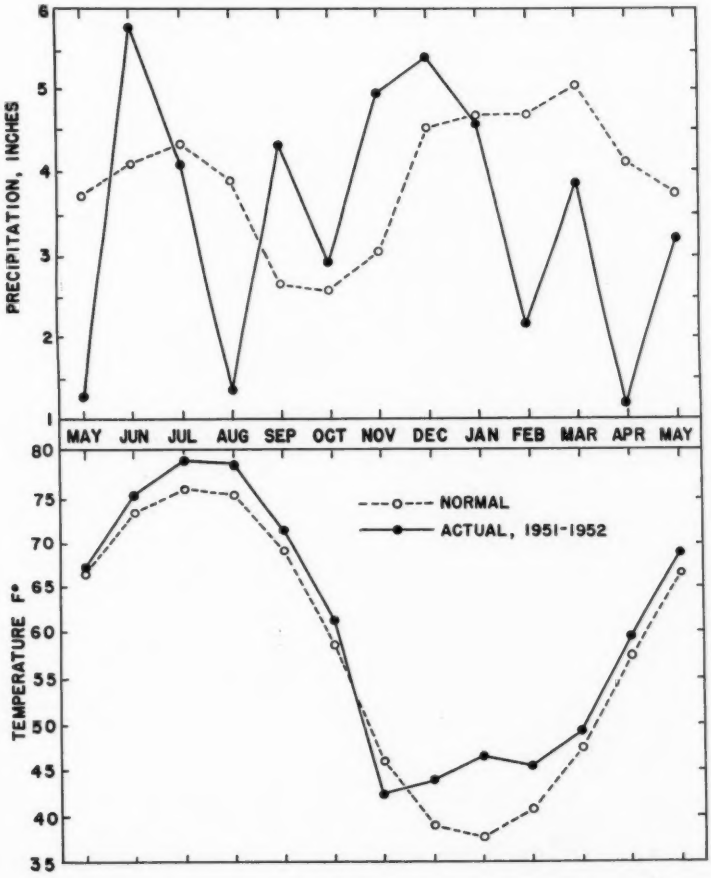

Fig. 1.—Normal temperatures, normal precipitation and deviations from normal during the study period (1951-1952), based on official Knoxville Weather Bureau records.

firm enough to walk on without danger of getting wet or muddy feet, but became flooded during heavy rains.

Area 9—the carcass studied in this area was placed on a fairly flat horizontal rock outcrop. The exposed surface was roughly level with the surrounding soil surface, and was about 5 feet in diameter. The carcass on this rock was fully exposed to the rays of the sun on clear days.

During the interval May 7, 1951-May 14, 1952, a total of 43 dog carcasses yielded significant information concerning seasonal distribution of carrion insects and seral stages in carcass communities (table 1).

Dogs of both sexes and of various ages and breeds were used. Uniformity of size was striven for; however, the weights varied from 16 to 29 pounds. The carcasses were obtained at the city incinerator within 9 hours after death. All but 3 of these specimens were killed by the injection of strychnine. The 3 exceptions were numbers 17 and 22, both killed by automobiles, and number 31, which was shot.

Strychnine is neither stimulant nor toxic to insects (Brown, 1951). That little strychnine remained in the carcasses is indicated by the work of Hatcher & Eggleston (1917) who showed that large amounts of strychnine are destroyed early in the putrefaction of mammals and that traces remain for long periods.

Evidence indicates that the presence of strychnine in the carcasses had little, if any, effect upon the community. The seres occurring at each of the 3 non-strychnine-killed carcasses were compared with those occurring at

TABLE 1.—Time of placement and location of carcasses

Carcass No.[a]	Date Placed (1951)	Area	Carcass No.[a]	Date Placed (1951-2)	Area
11	May 7	4	35	Aug. 15	4
12	May 7	5	37	Aug. 28	2
13	May 30	9	38	Aug. 28	4
14	May 30	4	39	Sep. 11	3
15	May 30	8	40	Sep. 11	1
16	May 30	5	43	Oct. 8	4
17	May 30	5	44	Oct. 8	2
18	May 30	7	46	Nov. 1	3
19	May 30	2	47	Nov. 1	1
20	Jun. 15	5	48	Nov. 30	3
21	Jun. 15	4	49	Dec. 12	1
22	Jun. 30	4	52	Jan. 4	4
23	Jun. 30	4	53	Jan. 4	2
24	Jun. 30	2	54	Feb. 11	3
25	Jul. 14	6	55	Feb. 11	1
26	Jul. 14	6	56	Mar. 14	4
28	Jul. 14	4	57	Mar. 14	2
30	Jul. 14	6	58	Apr. 9	3
31	Jul. 30	3	59	Apr. 9	1
32	Jul. 30	3	60	May 5	4
33	Jul. 30	1	61	May 5	2
34	Aug. 15	2			

[a] Missing numbers indicate carcasses only slightly studied.

other carcasses (strychnine-killed) with which they were paired in respect to study area and date of placement. In none of these cases was the difference between seres at the non-strychnine-killed and the strychnine-killed carcasses any greater than would be expected if all had been killed by strychnine.

The standard procedure was to place the carcasses in pairs in respect to date of placement. One member of each pair was placed in one of the wooded areas and the other was placed in one of the pasture areas. This procedure was designed to permit comparison of carcass seres in wooded areas with those in pasture areas. The pairs of carcasses were placed at intervals lasting from about 15 days in summer to about 35 days in winter (table 1).

Before intensive field work began it was learned that unprotected carcasses in the field were frequently disturbed, apparently by vertebrate scavengers. To prevent this disturbance wire cages were designed to fasten over the carcasses. The cages (22 x 14 x 7 in.) were made with 1 x 2 in. grid "turkey wire." The bottom of each cage was open. Each cage was held in place by 2 or 4 stakes driven into the ground, and each having in it a nail which hooked over a wire strand of the cage. The cages could be easily removed when carcasses were examined. Cages were used to cover all carcasses except those in a very dry condition.

EQUIPMENT AND PROCEDURES

Important equipment included an ordinary aerial insect net, a small entrenching tool for securing soil and litter samples, paper bags for samples, colorimetric soil pH testing kit, thermometer, insect killing bottles, rubber bulb aspirator for collecting small arthropods, assorted specimen containers, forceps, and a small loose-leaf notebook. For securing samples of flies present at carcasses, some special equipment was used. This consisted of a chloroform killing jar, an air-tight plastic bag (dimensions 13 in. square; open at one end), a foot-long leather thong, and a large handleless net. The circular wire hoop of this net was 2 feet in diameter, and had 2 bolt-secured joints to permit folding. The cone-shaped net bag was 4 feet long and olive drab in color.

Frequency of field trips varied from thrice daily (on certain occasions during the hottest weather) to once in 12 days (during a period of coldest weather). Usually, however, trips were made at intervals of one week or less. Several, but not all carcasses, were visited during each trip. The field trips were usually made between 11:00 a.m. and 3:30 p.m. Some visits were made before and after these times, including some made at twilight and during darkness, both in the early morning and late evening. Generally trips were made on the clearer days, however, a few were made during rain. In winter, trips were usually made on warmer days.

The kind and number of operations performed was variable and depended upon the condition of the carcass, whether or not detailed seral studies were being made, season of year, recency of previous trip, etc. Upon arrival several minutes were spent estimating the kinds and abundances of the various arthropods present on and in the vicinity of the carcass. The carcass was then turned over and the same done for the arthropods under it. A record

was made of the degree of bloating or deflation, moistness or dryness of the tissues, amount of skin and hair missing, exposed viscera and bones, odor, etc. Photographs were frequently taken to supplement the written records.

When flies were present in small numbers the ordinary aerial net alone was used to secure specimens of these insects. The use of the large handleless net was limited to times when flies were present in fairly large numbers. Samples were taken with this net at intervals of about 10 days or less. The following procedure was used when taking samples with the large net: The net bag was grasped at the apex and held high over the carcass. In this position the open end of the bag dangled about three feet above the carcass. The net was then suddenly lowered far enough to permit its open end to rest on the ground encircling the carcass. Still holding the apex of the net in one hand, the other hand was used to grasp and close the lower part of the net near the hoop. Then the portion of the net containing the entrapped flies was placed into the plastic bag containing an open chloroform killing bottle. Next the mouth of the plastic bag was closed by means of the leather thong. The flies were then removed and placed in a small labeled container.

Specimens of various insects which could not be identified in the field were often collected by hand, forceps, aspirator, or the ordinary aerial net. Large scale collection of most groups of insects was avoided, because it was desired to avoid undue disturbance of the community.

To determine kinds and estimate abundances of the numerous species of small arthropods which could not be identified in the field, samples of litter and soil were secured, placed in paper bags, and brought into the laboratory for examination. Each of these samples was taken from a square quadrat with sides 6 in. long. Each quadrat was located beside a carcass, with one of its sides touching the point of contact of the carcass with the ground. The sample taken from each quadrat consisted of the surface litter, and the soil to a depth of about 1 inch. These samples were taken most frequently during the stage of rapid decay following the bloated stage, for it was at this time that small arthropods were most abundant in the litter and soil. These samples were taken at intervals of about one week or less, except during the winter, when samples were less frequently taken (the longest interval between samples was 12 days).

A number of paired readings were taken of carcass temperatures and air temperatures. In determining the temperature a thermometer was placed so that the bulb was contacted above by the carcass and below by the ground. Corresponding air temperatures were secured by means of a shaded laboratory thermometer placed a distance of 2 to 5 yards from the carcass and about 6 in. above the ground. Forty-five paired readings were recorded between 11:00 a.m. and 4:00 p.m. on various days. Several readings were taken during each season of the year, and during each of the last three seral stages.

During the last week of June, 1951, colorimetric pH determinations were made of the soil in the various study areas. For these determinations, soil from about one-half inch below the surface was taken. The reading for each area ranged between 6.8 and 7.2, except for area 7 (pine woods), for which the reading was 5.8. Thirty-five readings were made of the soil

at a depth of one-half inch below various carcasses, only one reading being made for a carcass in any given seral stage.

During warm and hot weather the litter and soil samples were placed in the freezing compartment of a refrigerator to quiet the insects. Each sample was then placed in a sifter and shaken over a large piece of white plastic sheeting. Small arthropods fell onto the sheeting; larger ones were retained in the sifter. Representative specimens of the various kinds were collected and estimates made of the abundances of the remainder.

In the field, whenever possible, the actual number of insects seen was recorded. For those insects present in such large numbers that counting them was precluded, however, a 5-term scale similar to that used by Cantrall (1943) was used. The terms of this scale, arranged in order of increasing abundance, are: rare (i), scarce (ii), medium numbers (iii), common (iv), and abundant (v). In the section entitled "The Arthropod Members" the five-term scale is likewise used. There, however, the application of the scale is based upon an overall study of numbers observed in the field, numbers identified in the laboratory or by specialists, and a knowledge of the behavior of the various forms.

PHYSICAL ENVIRONMENT

SERAL STAGES

Mégnin (1894) divided the decomposition of human bodies exposed to air into eight stages. Johnston & Villeneuve (1898) arranged Mégnin's discussion in tabular form. Fuller (1934) divided the decomposition of sheep and cat carcasses into three stages, the last of which she states includes several of Megnin's later stages. Howden (1950) divided the decomposition of assorted carrion (partial and entire carcasses) into 2 stages. In the

TABLE 2.—Approximate duration of seral stages[a]

Season	General Locality[b]	Duration (days)			
		Average			Minimum
		Fresh	Bloated	Decay	Dry
Spring	Woods	4	7	26	90
	Pasture	2.5	4.5	13	75
Summer	Woods	0.9	3.5	11	50
	Pasture	0.9	2.5	10	50
Fall	Woods	7	9	34	80
	Pasture	2.5	11.5	21	80
Winter	Woods	25	20	95	?
	Pasture	8	32	85	?

[a] These approximations are based on field notes and photographs. Carcasses 15, 18, 26, 30, and 49, because of their "atypical" physical changes and/or because they were placed in "atypical" areas, are not included in these averages.

[b] "Pasture" indicates areas 3, 4, and 9. "Woods" indicates areas 1, 2, 5, and 6.

present investigation it was found convenient to divide dog carcass seres into 4 stages. Table 2 shows the approximate durations of the stages as they have been defined in this paper.

Fresh stage.—The fresh stage began upon death of the animal and continued until the early stages of bloating. Most carcasses were placed during mid- or late afternoon; during summer these carcasses sometimes showed signs of bloating by the next morning.

Bloated stage.—The bloated stage began during the early stages of bloating and ended when bloating ceased to be evident. In general, carcasses observed during cold weather did not become as strongly bloated as those observed during warm weather. All carcasses except 2 became more or less bloated. One exception, carcass 26, was completely skinned before being placed in the field. The other exception, carcass 49, underwent the first 16 days of its history during a period of very cold weather.

During winter the processes of "inflation" and "deflation" were gradual, each occurring over a period of many days. In summer, on some occasions, carcasses were observed to become strongly inflated within 48 hours after the onset of bloating. The deflation process was sometimes even more rapid; records were secured of 8 carcasses which on one day were strongly inflated, and on the next day completely deflated.

Decay stage.—The decay stage began when bloating had ceased, and ended when most of the remnants were relatively dry. The skin was usually broken in one or more places, permitting the entrance of air, and consequently facilitating the process of aerobic protein decomposition. This later process is referred to as decay by some bacteriologists (in distinction from putrefaction, or anaerobic protein decomposition [cf. Jordan & Burrows 1954]); therefore, I call this the decay stage.

Before the end of the bloated stage loss of hair from the intact skin had frequently begun. During the decay stage hair loss was frequently conspicuous. Hair loss was strongly correlated with the action of maggots: hair was almost completely lost from areas of skin where maggots manifested great activity; hair was not lost where maggots were not present; where maggots manifested medium activity, the hair was thinned. Maggot activity generally began where the eggs from which they hatched were laid, namely around the body openings (particularly the mouth), the throat (external), and on the underside of the carcass. In winter maggots did not progress to the upper portions of carcasses; consequently during this season those parts retained their hair. In summer certain carcasses were almost completely denuded of hair. The fallen hair formed a dense mat around many carcasses.

The soil under portions of many carcasses and within a radius of about a foot from these carcasses became pulverized to a depth of about an inch due to the burrowing action of arthropods (principally maggots).

Dry stage.—The limits of this stage are more difficult to define than those of the previous stages; this is due to the lack of pronounced events marking the beginning and end of the stage, and to the higher irregularity in the physical and biotic features. The stage began when only small amounts of decaying tissue remained, and ended when no carrion fauna remained. Usually a carrion fauna was present until only very scant (usually dry) portions remained. Actually carcasses sometimes were considered to be in the dry stage when, in fact, they contained considerable moisture; this moisture was gained mostly from rain, dew, or the underlying soil and litter. During this stage small amounts of semi-solid putrefying material were occasionally present on the ground under the solid remnants.

During the process of disintegration of the carcass ecosystem, there is an influx of non-carrion biota. If considerable amounts of dry portions remain, the carcass may become an ordinary "cryptozoic" niche (Cole 1946); in other words, the carcass remains may shelter fauna typically found under a variety of objects, such as boards, slabs of bark, and rocks.

TEMPERATURES

The results of the temperature readings are shown in fig. 2. Air temperatures (abscissas) are plotted against the corresponding temperatures under carcasses (ordinates). The rather wide dispersal of points is to be expected,

since air temperatures change more rapidly and fluctuate more widely than do temperatures under protected objects. The straight line running diagonally across the figure is the line on which all points would lie if air temperatures had always been equal to corresponding temperatures under carcasses. Points located above this line indicate carcass temperatures higher than air temperatures and points located below the line indicate carcass temperatures lower than air temperatures.

The few data from the air temperature range below 10° C are inadequate

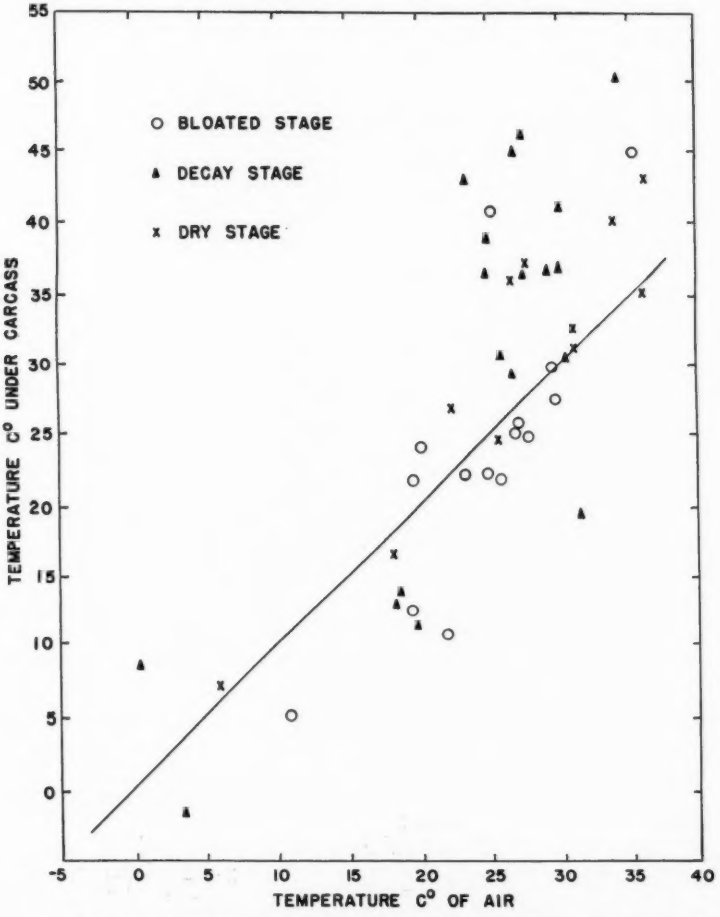

Fig. 2.—Relationship between air temperatures and corresponding temperatures under carcasses. If the former had always been equal to the latter, all points would lie on the diagonal line shown in the figure.

TABLE 3.—Approximate seral distribution of adult carrion-frequenting arthropods in summer[a]

Group (Adults)[b]	Stage[c]			
	Fresh	Bloated	Decay	Dry
Calliphoridae (G)	--xxxxxxxxxxx	XXXXXXXXXXX	XXXXXxxxx-----	------
Formicidae (G)	--------xxxxxx	xXXXXXXXXXX	XXXXXXXxxxxxxx	xxx---------
Muscidae (G)	----------xxx	xxxXXXXXXXXX	XXXXXXXxxx---	--
Sphaeroceridae (G)	--------xxx	xxxXXXXXXXXX	XXXXXXXXXXX	XXXxxxxxx--
Silphidae[d] (S)	-----xx	xxxxXXXXXXXX	XXXXXxxx----	----
Lepidoptera (G)	------	xXXXXXXXXXX	XXXXXxxxxx--	-----
Hymenoptera[e] (G)	-----	xxxXXXXXXXXX	XXXXXxxxxx--	-----
Sarcophagidae (G)	-----	xxxxxxXXXXXX	XXXXXXXXXxxxx	----------
Histeridae (G)	----	xxxxxxXXXXXX	XXXXXxxxxxxxx	----------
Staphylinidae (G)	-----	-xxxxxxxXXXXX	XXXXXXXxxxxxx	--------
Phalangiidae (G)	--------	-xxxxxxxxXXXXX	XXXXXXxxxx---	-----
Piophilidae (G)	------	-xxxxxxxxXXXXX	XXXXXXxxx----	----------
Araneae (G)	----------	-xxxxxxxxxXXXX	XXXXXXXxxxxxx	----------
Sepsidae (G)	----	--xxxxxxxxXXXX	XXXXXXxxx----	----
Phoridae (G)	-----	--xxxxxxxxxXXX	XXXXxxx------	----
Acarina (G)	----------	----------xx	xxxxXXXXXXXX	XXXXxxxx----
Nitidulidae (S)	--	----------x	xxxxXXXXXXXX	XXXXXXXxxx--
Cleridae (S)		-----	---xxxxxxxXXXX	XXXXXXxxx-
Dermestes caninus		-------	---xxxxxxxxxx	XXXXXXXxxx--
Trogidae (S)		--	--------xxxxxxxx	XXXXXXXXxx--

[a] Dashes indicate the smaller number of individuals and the greater probability of absence of the group at the time indicated.

[b] (G) indicates that insufficient information was obtained to permit determination of whether each species within the group illustrated had a seral distribution similar to the group as a whole. (S) indicates that each species in the group had a seral distribution similar to the group as a whole.

[c] Although each stage is given the same amount of space as the others in this table, it should be held in mind that each of the last three stages was longer than the one preceding it. For durations of stages see table 2.

[d] Excluding *Necrophorous pettiti*.

[e] Excluding Formicidae and Ichneumonidae.

for generalization. In the range of air temperatures between 10° and 25° C the carcass temperatures tend to be lower than air temperatures, while at higher air temperatures carcass temperatures tend to exceed air temperatures, this excess being more than 15° C in extreme cases. It is obvious that the microclimate in the vicinity of a carcass is often considerably different from the general habitat climate surrounding it and that nearby air temperatures offer only crude indication of temperature conditions under which many carrion-frequenting arthropods live.

HYDROGEN IN CONCENTRATION

The 35 pH readings of the soil at a depth of about one-half inch under carcasses during the various stages of decomposition were converted to hydrogen ion concentration. For each stage the mean hydrogen ion concentration was computed and reconverted to pH, thus giving a mean pH for each stage. These pH values are: Early bloated—7.1; late bloated—8.2; decay—7.9; early dry—7.7; late dry—7.3.

DYNAMICS OF THE COMMUNITY

SUCCESSIONAL PATTERN

The approximate seral distribution of adult arthropods in summer, with the omission of those forms of very little importance is shown in table 3. The approximate seral distribution of the more conspicuous larvae in summer is shown in table 4.

The following is a grouping of the various arthropods according to the seral stages during which they were most frequently found:[2]

Fresh stage.—Muscidae, Calliphoridae (particularly *Phaenicia caeruleiviridis* and *Phormia regina*).

Bloated stage.—Phalangiidae, Araneida, Silphidae†, Histeridae†, Staphylinidae† (particularly *Creophilus maxillosus, Ontholestes cingulatus,* and *Staphylinus maculosus*), Lepidoptera, Sphaeroceridae†, Muscidae† (particularly *Fannia* spp. and *Hydrotaea* spp.), Calliphoridae† (particularly *Callitroga macellaria, Phaenicia caeruleiviridis* and *Phormia regina*), Sarcophagidae, Hymenoptera.

Decay stage.—Phalangiidae, Araneida, Acarina†, Silphidae†, Histeridae† Staphylinidae† (particularly *Creophilus maxillosus, Ontholestes cingulatus, Staphylinus maculosus,* and small staphylinids), Nitidulidae† (*Omostia colon*), Lepidoptera, Phoridae, Sepsidae†, Piophilidae†, Sphaeroceridae†, Muscidae† (particularly *Fannia* spp.), Calliphoridae† (particularly *Callitroga macellaria* and *Phormia regina*), Sarcophagidae, Hymenoptera.

Dry stage.—Araneida, Acarina†, Staphylinidae† (small-sized individuals), Cleridae, Dermestidae† (*Dermestes caninus*), Nitidulidae† (*Omostia colon*), Trogidae†, Sphaeroceridae.

PERIODIC VARIATIONS IN ACTIVITY

Seasonal variations.—The peak arthropod populations and activity were in summer. They were smaller during spring and fall, and least of all during winter. On warm winter days a few adults of various species of the following groups were occasionally found active in the community (arthropods found only on rare occasions are excluded from the list): Acarina, Leptodiridae,

[2] Daggers (†) indicate forms which frequently occurred in fairly large numbers during the stage indicated. These forms might be considered "characteristic" for the designated stage.

TABLE 4.—Approximate seral distribution of conspicuous carrion-frequenting larvae in summer

	Stage			
Larvae	Fresh	Bloated	Decay	Dry
Calliphoridae	--xxXXXXXXXXXXXxxxxx------			
Muscidae	---xxxxXXXXXXXXXXXXXxxxxx-----			
Nitidulidae			--xxXXXXXXXXXxxx--	
Staphylinidae			--xxXXXXXXXXXxxx--	
Silphidae			--xxXXXXXXxxxx--	
Dermestidae				---xXXXXXxx-
Trogidae				--xXXXxx--

Histeridae (*Carcinops 14-striata*), Staphylinidae (small-sized individuals), Trogidae, Sepsidae, Piophilidae, Sphaeroceridae, Muscidae, Calliphoridae, Sarcophagidae, Formicidae, and Ichneumonidae (*Attractodes americanus*). On cold winter days only a few adult arthropods were found, and these were generally under carcasses and in an inactive state. Dipterous larvae, particularly those of Calliphoridae, were present in fairly large numbers throughout the winter. However, during the winter they rarely were found on the upper surface of carcasses, and, except during particularly warm periods, remained under or in carcasses.

Diel variations.—(1) Diurnal activity: The carrion fauna, as a whole, was most active during times of daylight. (2) Nocturnal activity: The following accounts pertain to observations made on four nights in July, 1951.

(a) Phalangids were actively capturing maggots. (b) *Silpha littoralis* f. *surinamensis*, all three species of *Thanatophilus*, and both species of *Necrophorous* were active. *Thanatophilus americana* and *T. noveboracensis* were observed mating. *Silpha littoralis* f. *surinamensis* and *T. americana* were observed feeding on maggots. All of these species took shelter rather rapidly when a flashlight was turned on. *S. littoralis* f. *surinamensis* was noticed to become active again very shortly after the flashlight was turned off. (c) Histerids were active in large numbers. (d) *Ontholestes cingulatus*, *Creophilus maxillosus*, *Philonthus cyanipennis*, and various small staphylinids were observed in activity. The first two mentioned were observed to take refuge rather slowly when the flashlight was turned on. (e) Trogids were seen, but, as in daytime, manifested little activity. (f) The geometrid moth, *Melanolophia canadaria*, was seen each night. Many were flying, others were perched on the wire cages or on the carcasses. (g) Adult Diptera manifested very little activity at carcasses. Only a few specimens of various kinds could be seen on or near carcasses. These specimens occasionally were on the wire cages. Kicking a carcass sometimes elicited a few buzzes from calliphorids. (h) Maggots were very active; they were in great evidence on carcasses and above the surface of ground litter. At carcasses in the sun on hot days, maggots were driven under the carcasses and deep under the shelter of ground litter, and at such times were little in evidence; night visits (or digging during the day) revealed their great abundances.

(3) Crepuscular activity: In general, the same species reported above as being active at night, were also observed in activity during dawn and dusk. In addition to the above-mentioned species, the sphingids *Amphion nessus* and *Sphecodina abbotti* were both observed active during dawn. Various species of adult flies began activity as daylight approached; the activity of these insects was reduced as darkness fell.

COMPARISON OF PASTURE AND WOODED AREAS

Insect populations in general were smaller at carcasses in pasture areas than at those in wooded areas. However, dermestids and clerids were distinctly more abundant in the pasture areas.

Ordinarily succession proceeded more rapidly in pasture areas than in wooded areas (table 2). Frequently it was noticed that maggots were more advanced developmentally at a carcass in a pasture area as compared with those at a carcass placed at the same time in a wooded area. These observations are consistent with those of Cole (1942) who found that an intact dog carcass placed on a grassy hillslope exhibited earlier evidence of insect activity than did a carcass with the abdominal cavity opened and placed in a wooded area. The normally greater insect activity at carcasses in wooded areas tended to hasten succession in those areas, but not sufficiently to counterbalance the effects of higher temperature in the pasture areas.

EFFECT OF RAIN

During the summer of 1951 five field trips were made during light to moderate rains. Observations on carcasses in the bloated and decay stages during these rains indicated no appreciable change in the tempo of insect activity—calliphorids and other Diptera continued to buzz in the air, while on the ground and on the carcasses various silphids, staphylinids, and other insects continued their feeding and mating activities.

FOOD RELATIONSHIPS

Probable food relationships in the community are illustrated in fig. 3. Carrion serves as the basic food for the community, with many arthropods feeding exclusively on it. Some arthropods feed upon other insects in addition to carrion. A small number of arthropods are exclusively predatory.

SUMMARY

This paper reports a study of dog carcass communities near Knoxville, Tennessee. Special emphasis has been given to the insects. The principal portion of the field work was conducted between May 7, 1951, and May 14, 1952. A total of 43 dog carcasses yielded significant information concerning seasonal distribution of carrion insects and seral stages in carcass communities.

Carcasses were placed at intervals of about 2 weeks in hot weather and less frequently during cooler weather. The standard procedure was to place carcasses in pairs with respect to date of placement. One member of each pair was placed on the ground in a wooded area and the other was placed in similar manner in a non-wooded (pasture) area; this pairing of carcasses was designed to permit comparison of carcass communities in wooded areas with those in non-wooded areas.

Frequency of field trips varied from thrice daily (on certain occasions during the hottest weather) to once in 12 days (during a period of coldest

weather). Usually, however, trips were made at intervals of one week or shorter. The type of operations performed upon visiting a carcass varied; important operations frequently included 1) recording physical condition of the carcass, 2) measuring air temperature and temperature under the carcass, 3) measuring pH of soil under the carcass, 4) counting various arthropods seen, or estimating their abundances according to a 5-term scale, and 5) collection of arthropods.

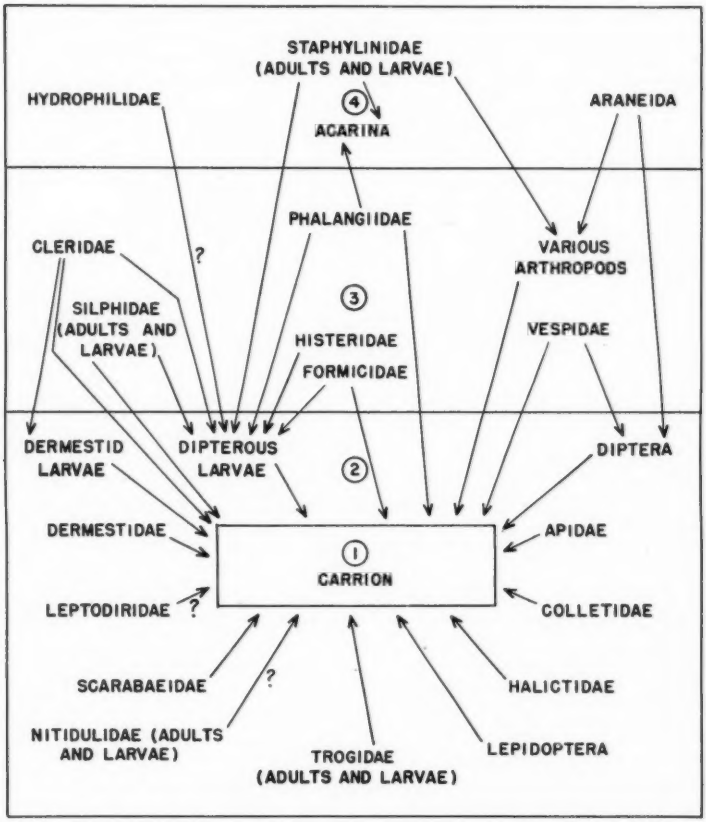

Fig. 3.—Probable food relationships in the carcass community. Lack of information prevents presentation of a complete or absolutely accurate picture. Various "trophic levels" are represented by carrion (rectangle 1), necrophagous species (rectangle 2), omnivores (rectangle 3), and predators (rectangle 4). Unless otherwise stated in the figure, reference is made to adults. The term "carrion" is intended to include all solid and liquid portions of a carcass. Question marks indicate families for which no definite evidence concerning the food relationships shown in the figure was obtained from field observations or published literature.

It was found convenient to divide dog carcass seres into the following 4 stages: fresh, bloated, decay, and dry. Each of the last 3 stages was of longer duration than the stage immediately preceeding it.

The shedding of hair by carcasses was found to be strongly correlated with the activity of maggots.

Points representing air temperatures plotted against corresponding temperatures under carcasses were rather widely dispersed. In the range of air temperatures between 10° and 25° C the carcass temperatures tended to be lower than air temperatures, while at higher air temperatures carcass temperatures tended to exceed air temperatures, this excess being more than 15° C in extreme cases.

Mean pH values of soil under carcasses during various stages of decomposition were: early bloated—7.1; late bloated—8.2; decay—7.9; early dry —7.7; late dry—7.3.

Considerable information was secured concerning seral distribution of adult and immature arthropods; tables are given showing these distributions. The data indicate an irregularity in the time of appearance of a particular species, but also indicate a regular pattern in the times of greatest abundances of many species.

Although arthropod populations were largest in summer and smallest in winter, certain species had their heights of populations during the cooler parts of the year.

Overall diel arthropod activity was greater than nocturnal activity. Many species (especially of Coleoptera) were active throughout the entire diel cycle. The activity of some species (especially of Diptera) was limited to diurnal intervals. Sphingids were mostly crepuscular in activity. The geometrid moth *Melanolophia canadaria* was solely nocturnal in activity.

Insect populations in general were smaller at carcasses in the non-wooded areas than in the wooded areas. Ordinarily succession proceeded more rapidly in pasture than in wooded areas.

A diagram is given illustrating food relationships.

Annotated List of Species

ARTHROPODA

The arthropods in the following discussion are considered to be members of the community because evidence suggests that they were attracted by conditions present in the carcass ecosystem and entered into competition there. This evidence for any particular species fell under one or both of the following headings: 1) knowledge of the biology of the species or of the taxonomic group to which the species belongs, and 2) observation of behavior of the species at the carcass. Certain forms (e. g., butterflies and wasps) made only brief (and sometimes recurrent) visits to the carcass. Other forms (e. g., silphids and histerids) spent several successive days at the carcasses. Still other forms (e. g., various mites) doubtless spent their entire lives there. All such species are included in the discussion which follows. The total of about 240 such species fell into 2 classes, 7 orders, 50 families, and 140 genera.

In the discussion of these arthropods certain information is presented in abbreviated form, as illustrated by the following example: "*Genus species* (Fab.): iv*, 22/III/52-6/XII/51; iv, 29/III/52-14/XI/51." The information given in these abbreviations is as follows, in the order presented: (1) Estimate of abundance of adults according to the five-term scale[3] (for species recognized in the field; in Roman numerals), or total number of specimens identified (for species not recognized in the field; in Arabic numerals). (2) Indication of whether adults were found in pasture areas only (one asterisk*), in wooded areas only (two asterisks**), or in both types of areas (no asterisk). "Pasture" refers to areas 3, 4, and 9; "woods" refers to areas 1, 2, 5, and 6. Areas 7 and 8, because of their departure from "typical conditions" are not included in either of the above 2 categories. (3) Seasonal distribution. The first date represents the earliest record that was obtained for adults during their season of activity, and the last date represents the latest such record. For certain species a 1952 date is given as the earliest record and a 1951 date as the latest record; this is due to the fact that field work was conducted during the spring seasons of both 1951 and 1952, and for the species concerned, the earliest record was secured during the 1952 season. Certain species were active only in cool or cold weather. The seasonal distribution for some species is listed as "entire year"; populations of all these species were smaller in winter than at other seasons. (4) Information concerning larvae (or other immature forms in the case of non-insectan arthropods). Following the semicolon the same pattern of abbreviated information given for adults is followed for larvae, except for the omission of item (2) in the sequence. No information for larvae indicates that larvae were not collected.

For certain groups or species various items in the above sequence are omitted when insufficient information is present, or when the inclusion of the item would be repetitious or otherwise of small value. Omissions are particularly prevalent for the larvae.

ARACHNIDA

The 23 species of arachnids included in this discussion fall into 3 orders, 14 families, and 19 genera.

PHALANGIIDA: ii, warm and hot weather; i.

Phalangids were occasionally seen on and in the vicinity of carcasses. At times they were observed capturing maggots and devouring the substance of carcasses. On one occasion two phalangids were observed struggling for possession of a large maggot. At another time a large individual of *Leiobunum ventricosum* ran from a carcass carrying a fragment of carrion on which were attached several maggots. Occasionally, as they crossed a carcass, they recurrently touched the carcass with their pedipalps (as if seeking a desirable feeding spot) and would finally begin feeding at some spot, such as an eye socket or the sole of a foot. Specimens collected during the interval May 2-July 3, 1951, are as follows (the quantity of specimens appears in parenthesis): *Leiobunum ventricosum* (Wood) (6), *L. verrucosum* (Wood) (4), *L. politum* (Weed) (2), and *Leiobunum* sp. (immatures) (5).

ARANEIDA: ii, entire year, ii.

A variety of spiders occurred at the carcasses. On many occasions they were seen devouring carrion-inhabiting flies. Once I observed a large spider running from a carcass with a large maggot. During the winter they were found in small numbers in an inactive state under carcasses. During the period May 1-December 31, 1951, the following spiders were collected (the quantity of specimens appears in parenthesis): Theridiidae.—*Asagena*

[3] See section entitled "Equipment and Procedures."

americana Emerton (1); Thomisidae.—*Coriarachme floridensis* Banks (1), *Xysticus elegans* Keyserling (1), *X. ferox* Hentz (6); Pisauridae.—*Dapanus mirus* Walckenaer (1); Linyphiidae.—*Epigerone banksi* Ivie and Barrows (1), *Walckenaera vigilax* Blackwall (1); Salticidae.—*Evarcha hoyi* Peckham (1), *Metaphidippus* new species (1), *Metaphidippus* sp. (juvenile) (1); Lycosidae.—*Lycosa hentzi* Banks (1), *L. rabida* Walckenaer (2), *Lycosa* sp. (immatures) (2); Oxyopidae.—*Oxyopes aglossus* Chamberlin (6).

ACARINA: v, entire year.

Soil samples taken beside carcasses frequently teemed with mites. At various times mites were piled in layers several individuals in thickness on the putrefactive substances under carcasses. Sometimes mites were distributed on the upper surface of carcasses at a density of 25 or more individuals per sq. in. They were most abundant during warm and hot weather, but during the winter a few mites could generally be found under each carcass. The surfaces of various adult and larval Coleoptera were frequently heavily laden with mites.

How far mites traveled to reach the carcasses is uncertain. Doubtless many of the species were present in the soil under a particular carcass at the time it was deposited. Their great abundances may have been due principally to rapid multiplication at the site of carcasses.

The following is a list of mites collected under, in, or on carcasses. Some of these species are known to be predatory; according to Edward W. Baker (communication) the remaining species on the list are assumed to be predacious because of their relationship to species better known.[4] The mites are as follows: Macrochelidae.—*Macrocheles* sp. (abundant); Parasitidae.—*Parasitus* sp. (abundant), *Pergamasus* sp. (scarce); Ascaidae.—*Asca* sp. (rare), *Gamasellus* sp. (rare); Zerconidae.—*Zercon* sp. (rare); Laelaptidae.—*Melittiphis* (?) sp. (rare); Discourellidae.—*Apionseius* sp. (medium numbers).

INSECTA

The total of about 217 species included in this discussion of insects occurred in 4 orders, 36 families, and 121 genera.

COLEOPTERA: v, entire year; v.

During the early decay stage Coleoptera vied with Diptera for dominance of the carcass community; during the late decary and the dry stages Coleoptera were distinctly the dominant forms.

HYDROPHILIDAE: i.

Most species of hydrophilids live in aquatic habitats, where they are principally scavengers and vegetation feeders. Comstock (1947) states that

[4] Non-predatory mites occurred under the carcass. but only in relatively small numbers; since these species may have either accidentally wandered into the community, or been present in the soil under a particular carcass at the time it was deposited, they are not included here. Instead, these species are rather arbitrarily listed in the section entitled "Accidental Species."

"some of the smaller species of this family are not aquatic, but live in moist earth and in the dung of cattle, where, it is said, they feed upon dipterous larvae." I found only two species of this family, both belonging to the genus *Cercyon;* according to Balduf (1935) the species of this genus build their egg cases in dung, damp earth or dead leaves.

Cercyon species 1: 30, 9/VI/51 - 10/VIII/51.

Cercyon species 2: 21, 2/V/51 - 7/VI/51.

SILPHIDAE: v; v.

Silphid larvae made their first appearances during the decay stage, generally about 6-8 days after the first appearance of adults. Their appearance frequently occurred at the time when large numbers of maggots were transforming to the pupal stage. Larvae of various instars and of various species occurred side by side. The larvae feed upon carrion. I have one record of a large larva of *Silpha littoralis* form *surinamensis* feeding upon a maggot. The adults are predators on maggots and in addition feed upon carrion.

Necrophilus pettiti Horn: i**, 7/II/51 - 9/III/52. I found these beetles only under carcasses. They seemed to be slower in movement than the other silphids. They generally did not attempt to hide when I exposed them by turning a carcass over. This is the only silphid which was found in association with a carcass in the late part of the dry stage.

Silpha littoralis form *surinamensis* (Fab.): v, 9/IV/52 - 19/IX/51; v, 9/IV/52 - 28/IX/51. The adults of this species seem to differ from the other silphids observed in being 1) more alert and quicker to hide, 2) more rapidly-moving, 3) more likely to be found in the cranial cavity of a carcass, and 4) more inclined to hide between loosened hair and the skin of a carcass. They have the tendency, more than Thanatophilus species, to work their way under a carcass. When scurrying over dried leaves they create an audible patter. On one occasion, upon lifting a patch of loosened hair from a carcass in the decay stage, a "handfull" of these insects was found aggregated in a small area. On several occasions large larvae of this species were found squirming in semi-liquid putrefying substances under carcasses; whether the larvae habitually entered this medium or entered it only when disturbed is not known.

Clark (1895) and others have observed adults of this species feeding upon maggots; I have seen them doing this on many occasions. On one occasion I observed a specimen crawl over the surface of a carcass, alternately pick up and drop three maggots and finally proceed to devour a fourth one. At times their abdomens became considerably engorged with food. Davis (1915) reported seeing adults feeding on the tissues of the leg of a porcupine. As previously mentioned, I have one record of a large larva of this species feeding on a maggot. The larva held the squirming maggot with its front legs while biting it with its mandibles.

On July 4, 1951, I brought about 30 adults into the laboratory for morphological studies. In the glass container the beetles paired and copulated repeatedly. As the males attempted to gain their position, some of the females struggled violently, others feebly, and still others not at all. The males, with their fore and middle legs, generally grasped the females at

the base of the elytra. While in copula they were not easily disturbed by shaking the glass container. They remained in copula for about one minute, after the termination of which the male retained his position on the female for about one additional minute (these time intervals were crudely estimated).

While preparing most of the above-mentioned specimens for study I cut off the wings near their bases. During this operation each specimen would generally squirt from the anal opening a brownish liquid. This liquid would travel about 3 in. upward or about 10 in. horizontally, depending upon the direction of ejection.

The biologies of the three species of *Thanatophilus* found at the carcasses have many similarities. Dorsey (1940) observed both adults and larvae of all three species feeding on decaying flesh. In the laboratory larvae of all three species refused maggots which he offered them. In the field I have observed the adults of all three species feeding on maggots. At my study carcasses the adults of all three species were present in approximately equal overall abundances. The species are:

Thanatophilus americana (L.): iv, 29/III/52 - 28/IX/51; iv, 29/III/52-22/IX/51. Generally, when these insects were common at a carcass, several pairs were seen, a male mounted on a female. However, these pairs usually were not in copula. Frequently such pairs, due to muscular movement of the female, rocked from side to side, at a rate of roughly 3 times per second; during this motion the top of the male moved in an arc of roughly one-eighth of an inch. A male frequently retained his position on a female, without copulation, for as long as the pair was observed, sometimes more than 15 minutes. Upon examining one of the pairs closely, I found that the male had its front legs resting on top of the pronotum of the female and the ends of its middle and hind legs hooked under the elytra of the female. On a few occasions I found one male mounted on another male, which in turn was mounted on a female; a "triple-deck" affair was thus formed.

At various instances upon being disturbed, adults would conceal their head and bright yellow thorax under leaf litter in ostrich-like fashion, leaving the dark-colored remainder of the body exposed.

The larvae of this species seemed to be more agile than those of any of the other silphids observed. In the shaded areas they sometimes climbed to heights of a foot or more on vegetation near a carcass. Newly-captured larvae generally made violent attempts to escape. Once, upon placing a large larva on a wet glass surface, I noticed that concurrent with a rapid movement of the legs there was a leech-like shortening and lengthening of the abdomen.

Despite the fact that adults of all three species of Thanatophilus were approximately equal in abundance, larvae of this species were much less commonly seen than those of the other two species of this genus; I have no explanation for this.

Thanatophilus inaequalis (Fab.): iv, 18/II/52 - 26/VI/51; v, 25/II/52 - 26/VI/51. This species, and the following species (*T. noveboracensis*), abruptly disappeared from the carcasses early in the season, a fact which I cannot explain.

Thanatophilus noveboracensis (Forst.): iv, 18/II/52 - 22/VI/52; vi, 25/II/51 - 4/VII/51. Once, while in the laboratory examining a soil sample

collected beside a carcass, I saw a male of this species mount (without copulation) a female even though both individuals had been dormant about 10 minutes previously due to cooling in the freezing compartment of a refrigerator.

Necrophorous spp.: ii. Members of this genus frequently bury small animal carcasses; the buried carcass serves as a source of food for the larvae. No evidence of attempts to bury dog carcasses was seen. The fact that I found no larvae of this genus might be correlated with the fact that there was no buried source of larval food. Steele's (1927) data indicate that adults of each of the two species prefer fly larvae to carrion, although he observed them consuming both. When I found these insects they were generally under carcasses. The two species observed are as follows: *Necrophorus tomentosus* Web.: ii, 28/V/52 - 14/IX/51; *Necrophorous orbicollis* Say: ii, 22/IV/52 - 17/IX/51.

LEPTODIRIDAE: iii.

Members of this family possess close affinities with the Silphidae; they have been placed in that family by some authors. Edwards (1949) and Blatchley (1910) indicate that these insects are to be found beneath dead bark or in rotten wood, decaying vegetable matter, and decomposing fungi. I found each species on and under carcasses, as well as in litter near carcasses.

Catops gratiosus Blanch.: iii, 17/X/51 - 1/VI/52. This species was found principally during cool and cold weather. On some occasions when they were abundant they were seen running over the carcass and aggregated in large numbers near the body openings, particularly the anus. If a carcass was shaken, they dropped quickly or ran from the carcass and took shelter.

Catops terminans LeC.: 36**, 5/IV/51 - 29/VI/51.

Prionochaeta opaca Say: 45**, 19/VI/51 - 30/VII/51.

HISTERIDAE: vi; vi.

During warm and hot weather, no carcass community passed through its stages without the presence of histerids. A number of species of histerids have been reported feeding on coleopterous and dipterous larvae inhabiting carrion and dung (Balduf, 1935). On many occasions I have observed them devouring maggots.

Acritus fimetarius LeC.: 1*, 14/I/52.

Atholus sedecemstriatus Say: 14**, 9/VI/52 - 25/VIII/51.

Carcinops 14-striata Steph.: 33, 11/VI/51 - 9/III/52. Thirty or more individuals of this small species remained under a carcass in the dry stage throughout the winter.

Hister abbreviatus Fab.: 64, 1/V/51 - 23/IX/51.

Hister coenosus Er.: 27, 9/VI/51 - 25/VIII/51.

Hister depurator Say: 3, 3/VII/51 - 15/VII/51.

Hister incertus (Mars.): 3*, 18/II/52 - 23/III/52.

Hister servus Er.: 2**, I/VI/51 & 19/VI/51.

Margarinotus cadaverinus Hoffm.: 17, 19/IV/52 - 21/VI/51.

Margarinotus stygicus LeC.: 1**, 10/VII/51.

Phelister vernus Say: 3*, 24/VI/51 - 6/IX/51.
Saprinus assimilis Payk.: 257, 16/IV/52 - 6/VIII/51.
Saprinus comformis LeC.: 4**, 16/V/52 - 24/VIII/51.
Saprinus lugens Er.: 5, 16/VI/51 - 13/IX/51.
Saprinus semistriatus Scriba: 18, 17/IV/52 - 3/VIII/51.
Saprinus vescus Mars.: 3*, 15/VI/51 - 5/XI/51.
Xestipyge conjunctum Say: 3, 16/III/52 - 5/XI/51.

STAPHYLINIDAE: v, entire year; v.

Various staphylinids thrive in many types of waste matter, such as carrion, manure, dung, fungus, offal, and under logs. Predatism is common among both the adults and larvae. Edwards (1949) states that ants and Diptera serve as the chief prey. According to Balduf (1935), in the great majority of records for free-living species, the food consisted of the larvae of muscoid flies, mostly taken from the carcasses of small quadrupeds. I have frequently observed adults feeding on dipterous larvae. On warm winter days I found various species of small staphylinids active under carcasses.

Aleochara lata Grav.: iv, 14/I/52 - 20/X/51.
Aleochara lustrica Say: 45, 22/IV/52 - 15/XI/51.
Baryodma sp.: 12, 6/V/51 - 31/XII/51.
Falagria dissecta Er.: 42, 18/V/51 - 6/X/51.
Belonuchus sp.: 14, 20/IV/51 - 1/XI/51.

Creophilus maxillosus L.: vi, entire year. I found adults of this species active as late as December 15, 1951. On January 1, 1952, an almost dormant individual was seen under a carcass. In the spring of 1952 they did not appear in appreciable numbers until April 4. Adults of this species were observed in greatest abundance at carcass 19 (in area 2) during the decay stage on June 5, 1951. On this occasion the leaf litter and the ground were moist. Maggots were abundant on the carcass and in the surrounding soil and litter. *Creophilus maxillosus* and another large staphylinid, *Ontholestes cingulatus,* were each present at a density of about 8 individuals per square foot of soil surface over an area of radius about one yard around the carcass. For an additional 4 feet on the surface of the soil in all directions from the carcass these two species were conspicuous.

Creophilus maxillosus was frequently observed devouring maggots. On one occasion an adult was seen devouring an apparently freshly-killed adult of the fly *Ophyra aenescens;* whether the staphylinid caught and killed the fly was undetermined. On another occasion one was observed devouring a medium-sized larva of *Silpha littoralis* form *surinamensis.*

Pairs of this species were frequently observed in copula. Usually, before copulation began, the females fled the males. Copulation began quickly after the males had caught the females. Frequently the female continued running during copulation. Often, at such times, the female ran under twigs or other obstacles, dislodging the male and dragging him behind her, their bodies facing in opposite directions and being connected only by the genitalia. The struggling male was occasionally dragged more than a foot in such manner before the pair separated.

On several occasions one member (male or female) of a copulating pair

was observed to continue devouring a maggot. On one occasion the male and female each was consuming a different maggot.

Gyrohyphus hamatus Say: 4**, 5/V/51 - 6/IX/51.

Ontholestes cingulatus Grav.: v, 17/III/52 - 25/X/51. For the record of greatest abundance of this species see the discussion of *Creophilus maxillosus*. Adults of *O. cingulatus* are the most agile and "light-footed" of any of the beetles that I found at carcasses. Usually, when disturbed, individuals would seek cover like most other beetles; however, on many occasions, they flew instead. This is the only beetle which I found at carcasses which ever took flight when disturbed. They were able to take flight readily from a relatively flat surface, such as that presented by a carcass. When captured, adults usually made violent attempts to escape, biting viciously at any object with which they were held. In a killing jar they were constantly in rapid movement until overcome by poison fumes.

Philonthus aeneus ? Rossi: 11, 11/VI/51 - 25/X/51.

Philonthus blandus Grav.: 14, 25/V/51 - 30/X/51.

Philonthus cyanipennis Fab.: ii, 15/V/52 - 19/X/51.

Philonthus inquietus Er.: 33, 31/V/51 - 31/XII/51.

Philonthus sericinus Hn.: 25, 18/IV/51 - 22/X/51.

Philonthus sp. near *basalis* Hn.: 2, 7/VIII/51 - 21/XII/51.

Philonthus spp.: 14 additional species of the genus *Philonthus* were collected; positive identifications could not be made for these species. They were grouped according to the various series set up by Horne (1884). The groupings of the species which I collected are as follows: Series A—1 species; Series B—4 species; Series C—3 species; Series D—5 species. A total of 240 specimens submitted for identification fell within these series; these specimens were taken at various intervals throughout all seasons of the year.

Quedius capucinus Grav.: 85, 18/V/51 - 31/XII/51.

Staphylinus comes LeC.: 30*, 16/VI/51 - 11/VIII/51.

Staphylinus femoratus Fab.: 44, 11/VI/51 - 11/VIII/51.

Staphylinus fossator Grav.: 8*, 21/VI/51 - 11/VIII/51.

Staphylinus maculosus Grav.: iv, 9/IV/51 - 25/XI/51. Although this species was present at most carcasses which underwent decomposition during its season of activity, it was never found in large numbers; usually only one or two specimens were found at one time. When disturbed this species sought refuge under the carcass or under ground litter. If the material under which specimens were hiding was removed, they frequently remained motionless in full view. Individuals generally struggled very little when captured. They were clumsy when taking off in flight, and usually climbed part way up the slender stem of some plant before attempting flight. Often at the first attempt they fell to the ground and were not successful until the second trial.

Staphylinus mysticus Er.: 1*, 13/V/51.

Aderocharis corticinus Grav.: 3*, 8/VI/51 - 24/VIII/51.

Rugilus angularis Er.: 19, 6/IV/51 - 31/XII/51.

Sciocharis sp.: 5**, 18/V/51 - 24/VIII/51.

Tachinus fimbriatus Grav.: 6, 5/IV/51 - 17/XI/51.

Tachinus flavipennis Dej.: 11, 19/VI/51 - 20/X/51.

Tachinus pallipes Grav.: 4, 4/V/51 - 31/XII/51.
Lesteva sp.: 2**, 8/VII/51 & 5/XI/51.
Megarthrus sp.: 7, 9/IV/51 - 6/IX/51.
Omalium sp.: 5**, 7/VI/51 - 6/XII/51.
Oxytelus insignitus Grav.: 41, 7/I/52 - 31/XII/51.
Oxytelus sp.: 1**, 11/VI/51.

CLERIDAE: ii.

I found 2 species of Cleridae at the carcasses, namely *Necrobia ruficollis* and *N. rufipes*. These 2 species are cosmopolitan as well as sacrophagous and predacious (Knull, 1951).

Necrobia ruficollis (Fab.): ii, 26/VI/51 - 5/XI/51.

Necrobia rufipes DeG.: ii, 5/V/52 - 9/X/51. This species has been recorded as a predator on the cheese skipper and dermestid larvae (Knull, 1951).

DERMESTIDAE

Dermestid adults and larvae both occur in a variety of places, usually where they can feed upon materials composed of skins, bones, hair, or feathers.

Dermestes caninus Germ.: v, 23/III/52 - 12/XIII/51; v, 29/III/52-20/X/51. My observations in the field indicate that this species feeds principally upon dried muscular tissue. I saw no evidence that they consumed appreciable quantities of skin. Instead, when consumable muscular tissue was covered with skin, these insects bored holes about 4 mm in diameter through the skin; through these holes, both adults and larvae gained access to the muscular tissue.

NITIDULIDAE

According to Edwards (1949) a few genera of Nitidulidae (*Nitidula* and *Omostia*) are ". . . seldom found anywhere except on or near the dry carcasses of dead animals, with most of the species living and breeding in carrion."

Nitidula bipunctata (L.): 2, 9/IV/52 & 1/V/51.

Nitidula flavomaculata Rossi: i*, 31/XII/51 - 25/IV/52.

Nitidula rufipes (L.): 1**, 9/IV/52.

Omostia colon L.: v, entire year; v. This was the most abundant beetle found at the carcasses. In regard to its food habits, Blatchley (1910) states that ". . . it was found on flowers of skunk cabbage in April; beneath bones and skin of dead calf in June and July, and on dry fungi in autumn, so that it may be said to be omnivorous in taste."

SCARABAEIDAE: ii.

One of the 2 large categories of scarabaeids consists of species which feed on dung, manure, excreta, waste, skin, feathers, carrion, etc. All of the species which I took at carcasses belong to this category.

Ataenius platensis Blanch.: 5, 7/V/51 - 23/IX/51.

Ateuchus histeriodes (Web.): ii, 3/V/51 - 9/X/51.
Dialytes striatulus (Say): 2**, 30/VIII/51 - 23/IX/51.
Geotrupes blackburnii Fabr.: 5, 16/I/52 - 31/XII/51.

TROGIDAE: iv; iv.

Trogids are characteristically found at animal carcasses, portions of which they use as food. They are slow-moving insects. When disturbed they usually draw in their legs and antennae and lie motionless. On rare occasions I have seen individuals attempt to hide by slowly burrowing under ground litter. The larvae were frequently found (in their burrows) under carcasses.

Trox monachus Hbst.: iv, 23/II/52 - 31/XII/51; 26/IV/52 - 15/XII/51. This was the most common trogid occurring at the carcasses. Very often I saw these insects in motionless pairs, a male mounted on a female, not in copula.

Trox suberosus Fab.: iii, 22/V/52 - 5/XI/51.
Trox unistriatus Beauv.: iv, 6/V/52 - 16/IX/51.
Trox sp. (*T. variolatus?* Melsh.): 2*, 2/V/51 & 15/IX/51.
Trox sp. (probably *T. hamata* Robinson): 5*, 22/V/51 - 26/VII/51.

LEPIDOPTERA: iii; i[5]

A number of species of Lepidoptera were attracted to the carcasses. Many species that occurred escaped capture. Microlepidoptera occurred in litter under carcasses, but due to lack of evidence that they were attracted, a discussion of them is omitted here. Specimens of each species in the following list were observed in contact with carcasses. Each species, except those indicated by footnote, was observed sucking liquids exuding from carcasses.

PHALAENIDAE

Psychomorpha epimenis (Drury): i, 22/III/52 - 4/V/52.

THYRIDIDAE

Thyris lugubris Bdv.: ii, 17/IV/52 - 17/VI/51.

SPHINGIDAE

Sphingids fly mostly at dawn and dusk. Since I was rarely in the field at these times, my estimates of their abundances may be very inaccurate.

Amphion nessus (Cr.): ii?, 2/VI/51 - 3/VII/51.
Sphecodina abbottii (Swainson): ii?, 24/VI/51 - 3/VII/51.

GEOMETRIDAE

Melanolophia canadaria Gn.: iii?, 1/VII/51 - 17/VII/51.[6] This moth

[5] The few lepidopterous larvae found are listed in the section entitled "Accidental Species."
[6] I did not observe this species feeding at carcasses.

was observed at each of the carcasses which I visited during 4 field trips made at twilight and darkness in July, 1951.

HESPERIIDAE

Proteides clarus (Cr.): i*, 19/VI/51 - 1/VII/51.[6]

PAPILIONIDAE

Battus philenor (L.): 1*, 14/IX/51.[6]
Papilio glauca L.: 1**, 29/III/52.

NYMPHALIDAE

Asterocampa celtis Bdv. & Lec.: iii, 14/V/52 - 15/IX/51.
Asterocampa clyton (Bdv. & Lec.): 1**, 25/VIII/51.[6]
Limenitis arthemis astyanax (Fabr.): 2**, 6/V/52 & 15/VII/51.
Polygonia comma (Harris): 1*, 23/V/52.
Polygonia interrogationis (F.): 6*, 23/V/52.

LYCAENIDAE

Everes comynatas (Godt.): 1*, 9/VI/52.[6]
Lycaenopsis argiolus pseudargiolus (Bdv. & Lec.): 3*, 23/V/52.

DIPTERA: v; v.

During the fresh and bloated stages Diptera were distinctly the dominant forms in the carcass community; during the early decay stage they vied for Coleoptera for dominance.

The number of adults of each sex was counted for one species of muscid (*Hydrotaea houghi*), all species of calliphorids, all species of sarcophagids, and one species of piophilid (*Prochyliza xanthostoma*) (additional information concerning these counts is given in the annotated list of species). For *Hydrotaea houghi,* the calliphorids, and sarcophagids, females greatly outnumbered the males, a fact which was probably associated with the deposition of eggs on the carcasses by the females. However, for *Prochyliza xanthostoma,* males considerably outnumbered females, a fact for which I have no explanation.

STRATIOMYIIDAE: i**; i.

Adult stratiomyiids are most frequently found on flowers and leaves; they are not ordinarily found at carrion. The larvae occur in a variety of situations, including privies, cow dung, and other decaying matter (Comstock, 1947). The larvae and pupae which I found occurred only under or in carcasses during the decay or dry stage in wooded areas.

Eulalia sp.: no adults; 2 15/IV/51 & 23/VIII/51.
Geosargus species 1: no adults 2, 26/VI/51.
Geosargus species 2: no adults, 4, 1/X/51.
Ptecticus trivitattus (Say): i, 19/VI/51-6/IX/51; 16, 26/VI/51 &

[6] I did not observe this species feeding at carcasses.

1/X/51. Occasionally adults of this species were seen hovering over carcasses or darting back and forth near carcasses. They usually returned to a carcass shortly after being driven away.

PHORIDAE i; i.

Phorid adults are particularly abundant about decaying vegetation, on leaves and windows, etc. (Curran, 1934). The larvae breed in dung, decayed vegetation, and dead animals (Peterson, 1951).

Diploneura cornuta (Lw.): 8, 3/VII/51 - 17/VIII/51.
Diploneura incisuralis (Lw.): 3**, 5/VI/51 - 11/VII/51.
Megaselia sp.: 7, 5/VI/51 - 11/VII/51.
Triphleba ? sp.: 1.**, 17/X/51.

SEPSIDAE: iii; iii.

Adult sepsids are found about excrement, carrion, and decaying vegetation (Curran, 1934). The larvae are primarily scavengers living in decayed vegetable matter, carrion, sewage, and filth (Peterson, 1951).

Meroplius stercorarius (Robineau-Desvoidy): 48, 6/VI/51 - 14/IX/51.
Nemopoda sp.: 14, 3/VII/51 - 20/VIII/51.
Sepsis neocynipsea Mel. & Sp.: 1*, 3/VII/51.
Sepsis punctum (F.): 10, 14/I/52 - 16/I/52, also 3/VII/51.
Sepsis pyrrhosoma Mel. & Sp.: 8, 5/VI/51 - 9/VII/51.

PIOPHILIDAE: v; v.

Adult piophilids are found about decaying organic matter, preserved meats, cheese. The larvae are, in general, scavengers. (Comstock, 1947).

Mycetaulus hornigi Cress: 248, 17/IV/52 - 13/IX/51.
Piophila casei (L.): 4*, 3/VI/51.
Piophila nigriceps Mg.: 26, 26/VI/51 - 15/IX/51.
Piophila privigna Mg.: 8, 15/V/51 - 23/VI/51.
Prochyliza xanthostoma Walk.: v, entire year. The 2 sexes of this species are readily differentiated in the field or laboratory by the shape of the head. Males outnumbered females throughout the year and at all seral stages. A count of 513 randomly selected specimens in the laboratory yielded 360 males and 153 females, or a ratio of 2.4 males to 1 female.

OTITIDAE: i; i.

Adult otitids are usually found in moist places (Curran, 1934). The larvae of some species are found in excrement (Peterson, 1941).

Euxesta notata (Wied.): 7, 1/VI/51 - 14/IX/51.
Chrysomyza demandata (F.): 3, 1/VIII/51 - 13/IX/51.

SPHAEROCERIDAE (=BORBORIDAE): iv, entire year; v.

Curran (1934) states that "the Borborids are almost always found about decomposing organic matter, in swampy places and about excrement." During the fresh and bloated stages I frequently found these flies collected about the

moist body openings. During the decay and dry stages they often gathered on the more moist parts of carcasses, and on many occasions were found aggregated in considerable numbers under the protection of fragments of skin.

Leptocera approximata Mall.: 3**, 5/VI/51 - 17/X/51.
Leptocera cellularis Sp.: 7**, 15/XI/51 - 30/XI/51.
Leptocera crassimana (Hal.): 3**, 31/VI/51 - 13/XI/51.
Leptocera exiguella Sp.: 5, 14/I/52 - 17/X/51.
Leptocera fontinalis (Fall.): 11, 26/IV/51 - 17/VIII/51.

CHLOROPIDAE: i; i.

Some chloropid species have been recorded living in excrement, in cast skins of larvae, and in dead insects (Peterson, 1951).

Chlorops certima Ad.: 1**, 6/VI/51.
Hippelates pallipes (Lw.): 2*, 30/VI/51 & 12/XI/51.
Oscinella soror (Maca.): 1*, 5/VI/51.
Tricimba trisulcata (Ad.): 1**, 6/VI/51.

DROSOPHILIDAE i.

Adult drosophilids are found around decaying vegetation, flowing sap, fungi, and ripe fruit (Curran, 1934). The larvae are frequently found in decayed fruit, fermenting milk, fungi, or products containing yeast (Peterson, 1951).

Amiota leucostoma Lw.: 1**, 2/VII/51.
Drosophila colorata Walker: 3*, 1/IV/51 & 8/VI/51.
Drosophila immigrans Sturt.: 2, 2/VII/51.
Drosophila melanica Sturt.: 1*, 2/VII/51.
Drosophila quinaria Loew: 1**, 26/VI/51.
Scaptomyza new species: 1**, 4/IV/51.

MUSCIDAE: iv, entire year; iv, entire year.

The maggots of a number of species of muscids breed in feces of vertebrate animals and within dead animal matter (Peterson, 1951).

Eremomyiodes cylindrica (Stein): 1*, 5/IV/51.
Fannia canicularis (L.): 6, 20/X/51, 16/I/52 - 23/III/52.
Fannia femoralis (Stein): 8, 2/VII/51 - 15/IX/51.
Fannia howardi Mall.: 13, 28/IV/51 - 1/VII/51.
Fannia leucosticta (Mg.): 1*, 3/VII/51.
Fannia sp. (*pellucida* Stein?): 1**, 16/VII/51.
Fannia sp. near *manicata* (Mg.): 8 pupae of this species were found under a carcass in a wooded area 10/VII/51.
Fannia incisurata (Zett.)?: 2*, 28/IX/51.
Fannia spp.: 7, 8/VI/51 - 24/X/51.
Hebecnema vespertina (Fall.): 1**, 27/II/52.
Hydrotata houghi Malloch: 473 (277♀♀, 196♂♂), 16/I/52 - 6/XII/51.
Hydrotaea occulta Meig.: 6*, 1/VI/51 & 6/VI/51.
Hydrotaea lata (Walk.): 12, 9/III/52 - 2/VII/51.

Hydrotaea unispinosa Stein: 2*, 26/IV/51 - 28/IV/51.
Hylemia sp.: 1**, 27/II/52.
Limnophora (*Gymnodia*) *arcuata* St.: 2, 14/I/52 & 9/III/52.
Morellia micans (Macq.): 14, 16/V/51 - 22/VIII/51.
Musca domestica L.: 71, 12/V/51 - 14/XI/51.
Muscina assimilis (Fall.): 3*, 21/XI/51 - 28/XI/51.
Muscina stabulans (Fall.): 1**, 24/VIII/51.
Ophyra aenescens (Wd.): 291 (189♀♀, 102♂♂), 4/III/52 - 14/X/51.
Ophyra leucostoma (Wd.): 373 (324♀♀, 49♂♂), 28/III/52 - 20/X/51.
Pegomyia affinis Stein: 1**, 15/VI/51.
Pegomyia lipsia (Wlk.): 1**, 19/VI/51.
Platycoenosia mikii Strobl.: 1*, 23/VII/51.

CALLIPHORIDAE: v, entire year; v, entire year.

Calliphorid adults were the most abundant flies present during the fresh and bloated stages. The larvae were present in tremendous numbers during the bloated and early decay stages. During the decay stage pupae were frequently found in large numbers under carcasses and in the soil near carcasses. For all species the females greatly outnumbered the males. The mean sex ratio of all species combined was 8.8 females to one male.

Calliphora livida Hall: 48♀♀, 27/II/52 - 15/XI/51.
Calliphora terrae-novae Macq.: 6♀♀*, 15/XI/51 - 21/XI/51.
Calliphora vicina (Robineau-Desvoidy): 35 (31♀♀, 4♂♂), 7/I/52-28/IV/52, & 21/XI/51.
Calliphora vomitoria (Linn.): 75 (67♀♀, 8♂♂), 17/X/51 - 5/V/52.
Callitroga macellaria (Fab.): v, 16/V/52 - 15/XI/51. A count of 609 randomly selected specimens in the laboratory yielded 501 females and 108 males.
Cynomopsis cadaverina (Robineau-Desvoidy): 58 (44♀♀, 14♂♂), 15/X/51-4/IV/52.
Lucilia illustris (Mg.): 66 (65♀♀, 1♂), 2/V/52 - 13/VII/51.
Phaenicia caeruleiviridis (Macq.): 1463 (1377♀♀, 126♂♂), 16/III/52-15/XI/51.
Phaenicia pallescens (Shan.): 108 (102♀♀, 6♂), 31/VII/51 - 10/X/51.
Phaenicia sericata (Mg.): 46 (41♀♀, 5♂♂), 21/II/52 - 15/XI/51.
Phormia regina (Mg.): v, entire year. A count of 797 randomly selected specimens in the laboratory yielded 708 females and 89 males. This was the most abundant species of calliphorid found at the carcasses.
Pollenia rudis (Fab.): 1♀*, 21/VI/51.

SARCOPHAGIDAE: iii, entire year: ii.

Female sarcophagids outnumbered males for all species, with the possible exception of *Sarcophaga sima*. For the latter species only 5 males were identified; females of this species may have been present among the 11 unidentified females of the genus Sarcophaga. The mean sex ratio, based on all specimens taken, was 5.3 females to 1 male. Since sarcophagids are alert and active flyers, the captures represented in the following account does not indicate the true number in which these flies occurred.

Chaetoravinia derelicta (Wlk.): 1♀*, 31/XII/51.
Chaetoravinia latisetosa (Parker): 2 (1♀, 1♂), 3/VI/51 - 15/XI/51.
Oxysarcodexia galeata (Ald.): 1♂ **, 3/VIII/51.
Ravinia ochracea (Ald.): 5 (3♀♀, 2♂♂)*, 23/V/52 - 14/IX/51.
Ravinia puisola (Wulp.): 6♀♀*, 6/V/51 - 15/XI/51.
Ravinia querula (Wlk.): 1♂*, 1/V/51.
Sarcophaga basalis (Wlk.): 1♂, 1/V/51.
Sarcophaga hunteri Hough.: 1♂*, 11/V/51.
Sarcophaga sima (Ald.): 5♂♂, 22/IV/51 - 6/VI/51.
Sarcophaga rapax (Wlk.): 2♀♀, 5/IV/51 & 16/V/51.
Sarcophaga spp.: 11♀♀, various dates.
Scarabaeophaga utilis (Ald.): 12 (11♀♀, 1♂), I/V/51 - 23/IX/51.

HYMENOPTERA: iv.

ICHNEUMONIDAE

Most species of ichneumonids have no association with carrion.

Attractodes americana (Ashm.): 16 (15♀♀, 1♂), 26/X/51 - 22/XII/51. These specimens were all taken *under* carcasses in the decay stage. This species has previously been taken from carrion (E. A. Chapin, communication).

FORMICIDAE: iv, all seasons.

Ants were sometimes present as scattered individuals on and under carcasses; at other times they formed large caravans, systematically transporting materials from carcasses. At various times I saw them feeding on liquids exuding from carcasses, transporting dead insects or fragments of a carcass, or struggling with dipterous larvae. The most common ant at the carcasses was *Prenolepis imparis*. This species was recorded in greatest abundance on April, 1951, at a bloated carcass. The ants were swarming at the eyes, vaginal orifice, and anus, and were present in large numbers on other parts of the body. Four records were secured of this species struggling with small maggots. Probably next in numbers at the carcasses was *Campanotus pennsylvanicus*.

Since ants normally occur in litter, it was frequently difficult to determine whether particular species were attracted by carcasses. The following species were found on or under carcasses, or were observed in the process of utilizing for food various materials obtained from the carcass ecosystem (the number of specimens collected is indicated in parentheses):

Ponerinae.—*Ponera trigona opacior* Forel (8), *Ponera* sp. (1).

Myrmecinae.—*Aphenogaster fulva* Roger (1), *Crematogaster lineolata* (Say) (26), *Crematogaster minutissima missouriensis Emery* (2), *Leptothorax curvispinosus* Mayr (4), *Myrmecina americana* Emery (10), *Monomorium minimum* (Buckley) (7), *Pheidole dentata* Mayr (10), *Pheidole* sp. (2).

Dolichoderinae.—*Iridomyrmex pruinosum* (Roger) (3).

Formicinae.—*Camponotus americanus* Mayr (rare), *Campanotus castaneus* (Latreille) (rare), *Camponotus pennsylvanicus* (DeGreer) (medium numbers), *Formica fusca* Linn. (scarce), *Prenolepis imparis* (Say) (common; occurred throughout year).

VESPIDAE: ii, warm weather.

The following vespids were observed capturing flies, gnawing at carcasses, and imbibing juices from carcasses:

Vespula maculata (F.): ii, 4/V/52 - 20/IV/51. On June 17, 1951, I recorded the activities of a bald-faced hornet capturing a fly. The hornet lit at two or three places on the carcass, quickly seized a fly, and flew to the height of about 5 feet in a nearby shrub. In the shrub the hornet hung by its right hind leg from a tendril of a grape vine which was supported by the shrub; here the hornet proceeded to chew on the fly. While its left hind leg dangled, the hornet held the fly with its middle legs, and manipulated it with its forelegs. Soon the head of the fly dropped to the ground. Duncan (1939) reports similar observations having been made of this species.

Vespula maculifrons (Buyss.): ii, 23/V/52-18/X/51. On two occasions I recorded this species eagerly imbibing blood oozing from the head of a carcass. Bromley (1931) likewise records blood as one of the observed foods of this species.

HALICTIDAE ii.

Augochlora striata Prov.: 2*, 9/IV/52 - 21/VI/51.
Augochlora pura (Say): 5**, 6/V/52 - 15/VII/51.
Halictus arcuatus Robt.: 1*, 9/IV/52.
Halictus stultus Cr.: 2*, 9/IV/52 - 12/IX/51.
Halictus zephyrus Sm.: 1*, 9/IV/52.
Halictus sp.: 1**, 15/VII/51.

COLLETIDAE

Colletes inaequalis Say: 1*, 9/IV/52.

ANTHOPHORIDAE

Anthophora aburpta (Say): 2**, 1/VI/51, 2/VI/51.

BOMBIDAE

Bombus impatiens Cr.: 1*, 2/VII/52.

XYLOCOPIDAE

Xylocopa virginica (Dru.): 3*, 8/V/52, 2/VI/51, 3/VI/51.

ACCIDENTAL SPECIES

There occurred in the carcass ecosystems a number of species of arthropods for which there was no evidence of attraction by conditions therein. Most of these species were rare; many were represented by only one or two specimens. Some of them were perhaps present at the site before the carcass ecosystem was established; others may have accidentally wandered there. The following is a list of these species (unless indicated for particular species, only adults were found):

ACARINA: Acaridae.—Caloglyphus sp.; Camisiidae.—*Platynothrus peltifer* (Koch); Eremaeidae.—*Ceratoppia bipilis* (Herm.); Eupodidae.—*Penthaleus major* (D.); Malaconotridae.—*Malacanothrus* sp.; Oribatei.—genus and species undetermined (nymph); Ixodidae.—*Dermacentor variabilis* (Say).

ORTHOPTERA: Acrididae.—*Chortophaga viridifasciata* (Deg.), *Melanoplus differentialis* (Thos.), *Melanoplus femur-rubrum* (Deg.), *Melanoplus scudderi scudderi* (Uhler); Blattidae.—*Ischnoptera deropeltiformis* (Brunner), *Parcoblatta uhleriana* (Saussure), *Parcoblatta* sp. (nymph); Gryllidae.—*Acheta assimilis* F.

ISOPTERA: genus and species undetermined.

NEUROPTERA: Ascalaphidae.—genus and species undetermined (larva); Hemerobiidae.—*Hemerobius* sp. (larva).

HEMIPTERA: Coreidae.—*Alydus eurinus* (Say), *Megalotomus quinquespinosus* (Say).

COLEOPTERA: Carabidae.—Harpalinae, genus and species undetermined (larva), *Oodes*? sp. (larva), genera and species undetermined; Cantharidae.—*Chauliognathus* sp. (larvae); Elateridae.—*Athous* sp. (*cucullatus* ? (Say)) (larva), *Ctenicera* sp. near *divaricata* Lec. (larva); Lagriidae.—*Arthromacra aenea* (Say).

LEPIDOPTERA: Olethreutidae.—genus and species undetermined (larva); Tortricidae.—genus and species undetermined (larva).

DIPTERA: Mycetophilidae.—*Mycomya littoralis* (Say) (larva); Psychodidae.—*Psychoda* sp. (larva); Ceratopogonidae.—*Dasyhela mutabilis* (Coq.); Scatopsidae.—*Scatopse notata* (L.); Melusinidae.—*Melusina* sp. (larvae); Tendipedidae.—*Hydrobaenus* sp. (larva); Tabanidae.—*Goniops chrysocoma* (O.S.) (larvae); Dolichopodidae.—genus and species undetermined (larva), genus and species undetermined (adult); Syrphidae.—*Mesogramma marginata* (Say), *Paragus angustifrons* (Loew) (larva); Psilidae.—genus and species undetermined (larva); Calobatidae.—*Calobatina geometroides* (Cress.); Ephydridae.—*Discocerina obscurella* (Fallen), *Notiphila* sp. (Fallen); Helomyzidae.—*Sullia quinquepunctata* Say; Muscidae.—*Stomoxys calcitrans* (L.); Scopeumatidae.—*Scopeuma furcatum* (Say), *Scopeuma stercorarium* (L.); Larvaevoridae.—*Acroglossa hesperidarum* Will., *Archytas aterrima* (Robineau-Desvoidy), *Chaetoplagia atripennis* (Coq.), *Epalpus signiferus* (Wlk.), *Gonia* sp., *Peleteria* sp., *Pseudotachionomyia aequalis* Rein., *Siphoplagiopsis similis* Tns., *Tachinomyia* sp. near *cana* Weber, *Winthemia rufopicta* (Big.), genus and species undetermined.

HYMENOPTERA: Braconidae.—*Apanteles carpatus* (Say), *Aphaereta muscae* Ashm., *Microtonus carabivorus* Mues., *Phaenocarpa* sp.; Cynipoidea—*Figites* sp. (Figitinae), *Trybliographa* (*Trybliographa*) sp. (Eucoilinae); Proctotrupidae.—*Phaenoserphus abruptus* (Say).

OTHER ORGANISMS

TURTLES: On June 8, 1951, at carcass 15 (in area 8, marsh) during the dry stage, 2 immature snapping turtles (*Chelydra sepentina* (Linn.))

(plastron lengths 6 cm.) were found just outside the cage protecting the carcass. The stomach of one of these turtles was examined for its contents, which were as follows: 4 silphid larvae, 157 calliphorid larvae, and 1 calliphorid pupa.

On 5 occasions I recorded Carolina box turtles, *Terrapene carolina* (Linn.), at carcasses. On two of these occasions the turtles had made their way under the cages. One of these latter turtles (an adult) was examined for its stomach contents, which were as follows: 1 small snail shell, 4 diplopods, 1 heteropteran nymph, 3 histerid adults, 4 staphylinid larvae, 5 silphid larvae, 1 *Silpha americana* adult, 1 trogid adult, 1 trogid larva, 3 newly-emerged calliphorid adults, several dog hairs, 1 distal phalanx of a dog, and other partly-digested materials.

FUNGI: Fungi (excluding bacteria) were occasionally conspicuous under (and, less frequently, on) carcasses. The following fungi which were identified from the carcasses doubtless represent only a small proportion of the total number of kinds which occurred: *Aspergillus* sp., *Coccidiodes immitis* R. and G., *Mucor* sp., *Penicillium* sp., *Scopulariopsis* sp., and *Syncephalastrum* sp.

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Utilization of Brown Fat During the Latter Stages of Pregnancy in Mice: Histological Analysis[1]

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Cramer's (1920) hypothesis that brown fat constitutes an endocrine organ has not been supported by demonstrations of its histological and physiological dissimilarity to known endocrine glands (Rasmussen, 1923; Fawcett, 1948, 1952). Littrell *et al.* (1944), Hook and Barron (1941), Mirsky (1942), Fawcett (1948), Fawcett and Jones (1949), and Baker *et al.* (1950) have indicated that brown fat is far more active metabolically than white "depot" fat and particularly sensitive to endocrine influence. Preliminary observations have indicated that brown fat is particularly responsive to physiological changes accompanying parturition. The present study is concerned with histological changes in the interscapular brown fat of the mouse from seven days prior to and eight days after parturition.

Acknowledgment.—I should like to express my deep appreciation to Dr. C. W. Nixon of Northeastern University for his interest and helpful guidance in this work.

Materials and Methods

Twenty-one C57/BL/6 strain mice, *Mus musculus*, 3 months or older were used. The time of estrus was determined by vaginal smears to establish the probable time of conception and parturition.

Three minims of a 1:6 normal saline dilution of Veterinary Sodium Nembutal (Abbott) per 20 g of body weight were injected intramuscularly as an anesthetic.

The scapular region was depilitated and brown fat was removed after making a transverse cut between the outer borders of the scapulae.

In all possible cases results of at least two matings of each female mouse are reported. The first mating and accompanying operation furnished tissue for the timed histological portion of the work; the second mating furnished data in evaluating any physiological effects of the removal of the brown fat. As a control, a simple exploratory operation was performed to determine if regeneration had occurred.

Histological changes were studied from haematoxylin and eosin stained sections. Alterations in glycogen were checked by the method of McManus (1946), mitochondria by the method of Mallory as modified by Lillie (1944), and lipids according to the Sudan Black B method of Lillie (1944). All sections were cut on the rotary microtome at 5 μ except those used for the lipid test, and these were cut on the freezing microtome at 10 μ.

[1] This paper is a revision of a thesis done in partial fulfillment of the requirements for Master of Science degree at Northeastern University, Boston, Massachusetts.

Tissue volume ratios were determined (Chalkley, 1943). The ocular diaphragm was equipped with four pointers, each in focus on the field. The section was systematically traversed by means of the mechanical stage. Note was taken in each field of the coincidence, or "hits," of the pointer tips on any of the following tissue fractions: brown fat cell nuclei, cytoplasm, and locules. Hits on other tissues or fractions thereof were disregarded. Counting was continued to at least 500 hits. Ratio of locule volume to cytoplasmic volume could be expressed as ratio of hits on locule to hits on cytoplasm. Such ratios are accurate if care is taken to count only those tissue fractions in focus at the pointer tips.

The brown fat of six mice was removed at times varying from 7 days to 1 day before parturition, and from eleven other animals at intervals up to 8 days post-partum. Four sham operated animals were used as controls.

All mice were maintained on a diet of Purina Laboratory Chow; food and water were available *ad libitum*. The mice were kept at a temperature of 21° C and were weaned at 21 days.

OBSERVATIONS

MORTALITY OF LITTERS FROM PRE- AND POST-PARTUM OPERATED MOTHERS

Controls.—Control animals underwent a sham operation 1 day before parturition. Thus, if post-operative shock were to occur, causing the animals to fail to nourish or otherwise care for their young, it should be exhibited in its full effect when the operation is performed as close to parturition as possible (table 1). All the young from the first mating of mouse 49 died before weaning, whereas all of the second litter survived. In view of the survival of the litters from three other control animals, it may be assumed that post-operative shock was not the sole cause of death.

Young which died, or were killed as a result of the mother's cannibalism, possessed little or no milk in their stomachs, possibly resulting from the inability of the mother to produce sufficient milk.

Experimental.—Results of the pre-partum operations are shown in table 2. Of the young from the first matings of pre-partum operated mice only seven of forty lived to be weaned. The average mortality was 82%. Of the twenty-one mice born as a result of second matings, ten, or almost half lived to be weaned. The mortality decreased to 52%. Chi-square homogeneity tests show that this difference is non-significant. However, the same test does

TABLE 1.—Successive matings of control animals which were "sham" operated one day before birth of young

Mouse No.	*First Mating*		*Second Mating*	
	No. born	No. alive at weaning	No. born	No. alive at weaning
54	6	4	9	3
59	6	6	7	7
69	8	8	4	4
49	6	0	6	6

TABLE 2.—Results of two successive matings of pre-partum operated mice

Mouse No.	Operation, days pre-partum	No. born	No. dead before weaning	Percent mortality
		First Mating		
21	7	8	8	100
17	5	7	4	57
7	3	7	3	43
5	3	6	6	100
63	1	6	6	100
13	1	6	6	100
		40	33	Av. 82
		Second Mating		
7	3	6	6	100
63	1	8	2	25
13	1	7	3	43
		21	11	Av. 52

indicate a significant difference in the mortality of the young of the pre-partum operated mothers when compared with the control group. Operations performed post-partum produced no significant effect on mortality in subsequent litters (table 3).

There are two common causes of mortality in young mice. There is usually some incidence of young dying from inherent causes before weaning in the C57/BL/6 strain, but this incidence is very low compared with the results obtained in this work. Therefore some other mechanism must be the cause. The results obtained from sham operated animals indicated that shock did not cause mothers to neglect their young; removal of the brown fat must have had some direct effect on the female's ability to nourish and care for them. Offspring died from lack of nourishment or were consumed by the mother. The former phenomenon would lend support to the theory that brown fat is related to pregnancy and may affect the production or quality of milk. This remains to be investigated.

Regeneration.—No significant differences exist between the mortality figures obtained for the control group and those observed in any of the second matings. The apparent increase in relative viability in these litters suggests the possibility of regeneration of the brown fat. To test this hypothesis most of the experimental mice were killed and the interscapular region examined. No regeneration of brown fat was noted in any mouse in 3 to 6 months. According to Auerbach (cited in Rasmussen, 1923) no regeneration of brown fat occurs in the rat. Instead, the area from which the brown fat is removed is filled with white fat. In this work also, a slight accumulation of white fat was found, but the interscapular area was mainly occupied by scar tissue and fascia.

HISTOLOGICAL

Depletion of brown fat.—Haematoxylin and eosin sections of the interscapular brown fat were prepared to determine the histological state at the time of excision.

At 7 days pre-partum the polyhedral brown fat cells contain numerous small locules varying from 2.2 μ to 4.6 μ in diameter. Observations on cells of the same tissue stained with Sudan Black B confirmed the assumption that these locules are mainly occupied by fat. The nuclei are eccentrically located among the several locules (figure 2).

Tissues taken on the 5th and 3rd days pre-partum showed a progressive increase in locule size from an average of 4.6 μ to 7.7 μ in diameter (figs. 7-9). This phenomenon was apparently produced by coalescence of the smaller locules, a process which gradually forced the nucleus towards the periphery of the cell. A simultaneous increase in the locule/cytoplasm volume ratio from 0.46 on the 7th day to 1.00 on the 3rd day was also observed. Thereafter the locule/cytoplasm ratio dropped abruptly to 0.42 on the 1st day post-partum. During the next 7 days the ratio rose with equal rapidity to 1.48 (figure 1). The decrease in locule/cytoplasm ratio near the time of

TABLE 3.—Results of two successive matings of post-partum operated mice

Mouse No.	Operation, Days post-partum	No. born	No. dead before weaning	Percent mortality
		First Mating		
67	8	7	1	14
65	8	6	1	17
6	8	6	2	33
57	6	5	0	0
50	6	5	0	0
68	4	6	3	50
62	4	8	2	25
58	3	6	2	33
53	2	7	7	100
64	1	5	0	0
60	1	4	4	100
		65	22	Av. 34
		Second Mating		
67	8	4	0	0
65	8	6	0	0
6	8	7	7	100
57	6	7	0	0
50	6	5	1	20
68	4	8	8	100
62	4	6	0	0
58	3	7	4	57
53	2	9	3	33
63	1	4	0	0
		63	23	Av. 37

parturition is accompanied by fragmentation of the large locules. During the post-partum period locule size rose from 1.5 μ to 7.7 μ in diameter. These data apparently reflect rapid but temporary depletion of depot fat accumulating during the latter third of pregnancy.

Association of brown fat and mammary glands.—A striking feature in these sections was the occurrence of ducts and secretory tubules embedded in the brown fat (fig. 4-6). Ehrmann in 1883 (cited in Rasmussen, 1923) described various inclusions in brown fat from the cervical region which he felt was accessory thyroid glands. Dalquest and Werner (1951), working with the tropical fruit bat, *Artibeus jamaicensis,* also observed ducts in the same locus. They did not identify these structures, but their interpretation lent weight to the hypothesis that brown fat is glandular in nature. Similar ducts and follicle-like structures were found in the present study. There are two reasons why the ducts could not be associated with the thyroid glands as suggested by Ehrmann. First, the sections of fat were taken from the interscapular region, much too distant from the normal site of the thyroid, and more important, these tubules displayed an apocrine type of secretion which does not occur in the thyroid. Apocrine glands do occur in the body as sudoriferous and mammary glands. These were not sweat glands tubules because they were found far beneath the subcutaneous tissue. Their histological characteristics and position make it seem certain that they are ramifications of mammary glands. The alveoli in which mammary ducts terminate may, in sectioned tissues, resemble follicular structures. Although Dalquest and Werner did not state the sexes of the fruit bats, it is possible that male

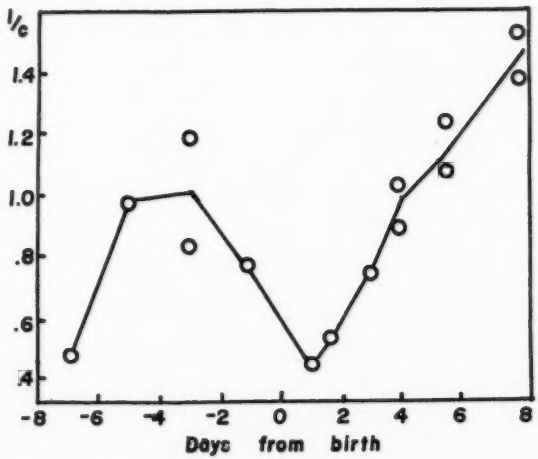
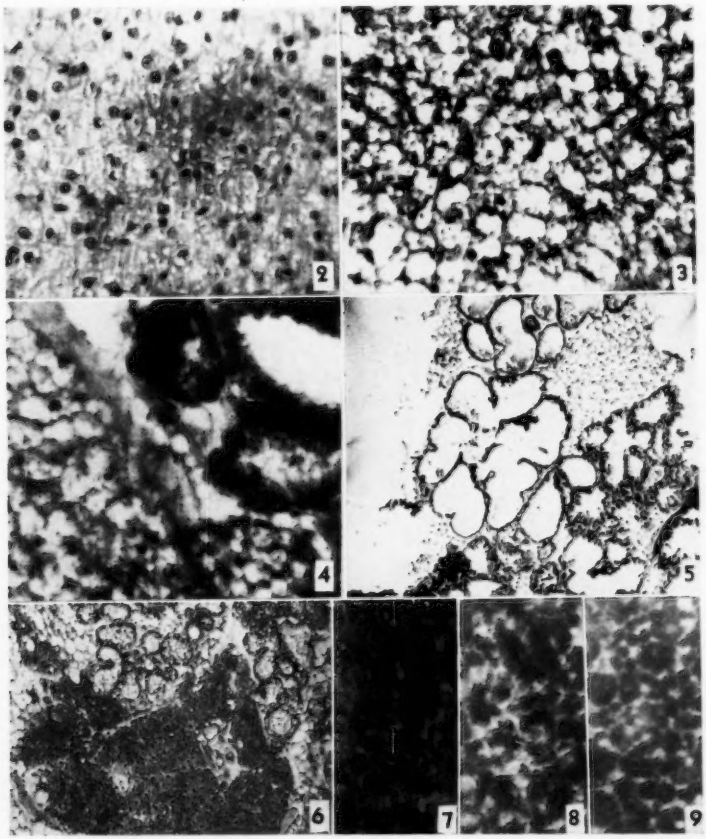


Fig. 1.—The locule/cytoplasm volume ratio of brown fat at varying intervals. Minus signs indicate days before and positive signs days after birth.

bats, as male mice, may also possess mammary tissue (Fekete, 1941). Fawcett (personal communication) expressed the belief that Dalquest and Werner actually found parotid gland ducts since this gland is very extensive in the fruit bat.

Mitochondria.—Recently (Green, 1954) reported that mitochondria through oxidizing enzymes play an important role in fat metabolism. Any change in their appearance might indicate active fat metabolism. The actual



Figs. 2-9.—2. Brown fat with abundant cytoplasm and small fat locules. ×350. 3. Brown fat with large locules and eccentrically located nuclei. ×350. 4. Brown fat with large locules. Note mammary alveoli on right side. ×350. 5. Low power of figure 4. ×90. 6. Low power of figure 2. ×90. 7, 8, and 9. Sudan Black B stain showing increase of fat droplet size. ×750.

number of mitochondria varied greatly from cell to cell although they were present in all tissues examined. But, as the number of days before parturition decreased, mitochondria became more evident until they could be observed throughout the cytoplasm. A continued increase was observed 1 to 8 days post-partum.

Glycogen.—With the exception of one mouse, glycogen was not found in brown fat. This mouse was operated on 8 days after parturition. The glycogen occurred in the cytoplasm in the form of irregularly disposed granular elements. Since all mice were operated on during the daylight hours, these findings agree with those of Fawcett (1948, 1952). He found that there was either a trace or no glycogen if the animals had an unrestricted diet, and their brown fat was removed during the light hours of the day. These results would indicate that the deposition of glycogen in brown fat was not affected by pregnancy.

DISCUSSION

The significant difference between the viability of the litters of the control animals and the first litter of pre-partum operated animals suggests that the ability of the mother to care for her young during the period immediately following birth is dependent upon adequate reserves of brown fat. This hypothesis is supported by additional data which indicate that brown fat is mobilized directly prior to delivery.

The results from the post-partum operated mice suggest that accessory brown fat areas hypertrophy and assume the function of the main interscapular mass, although this has not yet been demonstrated.

It appears that brown fat has a dual function in the metabolism of the mouse. The observations made on the reduced stomach milk content of the non-viable young, and of the proximity of the brown fat to the mammary glands, support the hypothesis that this fat is needed in milk production. Since there is little time for accessory brown fat deposits to hypertrophy before birth, the critical need seems to exist prior to parturition or during birth itself. Hence, a second function may be as a supply of energy to cope with the processes of delivery.

SUMMARY

Histological and physiological studies were made on the interscapular brown fat to determine its relationship to pregnancy in the house mouse, *Mus musculus*.

Interscapular brown fat of twenty-one mice was extirpated at intervals from 7 days before to 8 days following parturition; observations were made of the reactions of these mice towards the litters of two successive matings. Mortality among the litters of mice whose mothers were operated pre-partum averaged 82% of the first litter and 52% of the second litter. Mortality in the litters of those which were operated post-partum averaged 34% of the first litter and 37% of the second litter.

From 7 to 3 days prior to parturition there was an increase in vacuole size within the cells of the interscapular brown fat and a similar increase in lipid content. This was paralleled by a decrease in the amount of cytoplasm.

From 3 days before to 1 day after parturition a reversal of this trend was observed. Following this the initial process was repeated. Mitochondria followed the above cycle by becoming more evident in heavily laden brown fat cells. Except for a trace of glycogen in one section, none was found in the brown fat tissue. Mammary tubules were indentified in all sections.

The present study indicates that brown fat is simply another form of adipose tissue physiologically more active than white fat. The brown fat is highly mobile during pregnancy and lactation.

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Notes and Discussion

The Ichthyokinometer, an Improved Ichthyometer for Studying Action of Chemical Agents Quantitatively in Fish

Fish have long been used as test animals in pharmacological investigations. With few exceptions subjective qualitative analysis of drug action on fish has been predominant. Fish, such as the common goldfish (*Carassius auratus*) are more sensitive to many drugs than is the guinea pig (Lapenda, 1931). Attempts to record drug action on fish quantitatively include reports by Magnan (1929), Breder and Nigrelli (1935), Stanley and Teacher (1931), Macht (1930, 1943), Pittenger and Vanderkleed (1915, 1919, 1929) and Spencer (1929). The term "ichthometer" appears first used by Spencer to designate an instrument for recording the linear movements of fish. Later, Macht (1943) used a modification of this device for recording the analgesic action of morphine, cobra venom and saponins. The ichthyometer gives a curvilinear recording of the fish's movements which are difficult to measure quantitatively. The writers have adopted the term "ichthyokinometer" as more appropriate for a device recording muscular activity of the fish. An advantage of the recording device described here is the rectilinear recording which makes possible quantitative measurements by use of the planograph.

Description of the Ichthyokinometer

The ichthyokinometer is an ichthyometer essentially with two modifications consisting of 1) two low-friction pulleys arranged such that any pull on the cord by the fish is transferred to a vertical motion on the recording surface and 2) a glass bead mounted above the fish such that movement of the cord is directed downward (fig. 1). The movement by the fish is transmitted by a thread to a lever consisting of two paper "soda" straws fastened together at one end. A pin is pushed through the straw and into a cork forming an axle for movement. The cork is then held by a clamp on a ringstand. The length of the straw lever is 17 inches, the fulcrum being 12 inches from one end. The shorter end of the lever is attached to the recording device composed of two pulleys, a weight and a vertically moving writing lever. By carefully adjusting the weight of the counter weight the pull of the lever against the movement of the fish can be reduced to a minimum and the recording of the fish's activity will be greatly sensitized. The thread is attached to the skin of the fish by means of a needle which is carefully pushed through the skin below the dorsal fin which causes no inconvenience to the movements of the fish in the water. Recordings of the activity can be made with different speed kymographs One such kymograph which is well suited to this purpose is the "slow and fast" kymograph manufactured by the Harvard Apparatus Company which has a pendulum speed adjuster making possible very slow movement of the drum over several hours of time. This device may be set for a ten-hour run enabling one to record the long-time effects of a chemical agent or even diurnal rhythms in fish. Many factors may influence activity of fish other than specific drugs such as hydrogen-ion concentration, aeration of the water, temperature, light intensity, cyclic behavior, size of animal, etc. By using a known quantity of water the concentration of the drug used can easily be adjusted. If a large number of fish is used in an investigation, a marking system for identification of the fish becomes necessary (Adams and Hiestand, 1954). The procedure consists of injecting a small amount of India ink under the skin of the fish by means of a small hypodermic needle (No. 26 gauge). This mark does not harm the fish and will be visible for six to eight weeks. By using one or more black dots or by using other colored ink, various numbers or combinations of marks can be used effectively for innumerable markings of different designations with a large number of fish. No noticeable injury to the fish results from this method of marking.

Summary

A method has been described for recording the activity of fish. It consists of a modification of the ichthyometer and permits quantitative as well as qualitative recording of the influence of action of chemical agents on activity of fish. Because all movements

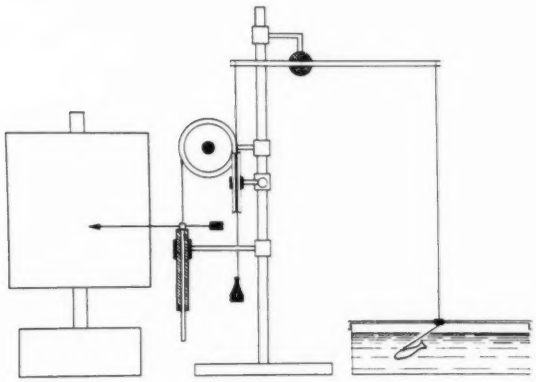

Fig. 1.—Diagram of the ichthyokinometer showing attachment to fish.

of the fish are recorded vertically instead of in a curvilinear fashion, the amount of movement can be measured quantitatively with a planimeter. The device has been called an ichthyokinometer.—THOMAS ADAMS, *Aeromedical Laboratory, Fairbanks, Alaska,* and WILLIAM A. HIESTAND, *Purdue University, Lafayette, Indiana.*

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The Guinea Worm, Dracunculus insignis (Leidy 1858) Chandler 1942, in a Raccoon, Procyon lotor, from Michigan, a New Location

This is the first report of *Dracunculus insignis* in Michigan. The material for this report comprises one female specimen collected by John Slee from the subcutaneous fascia of the inner thigh of a raccoon in Ingham County, Lansing, Michigan, Dec. 21, 1955.

This specimen measured 34.5 cm in length with a maximum diameter of 1.1 mm.

Previous reports of *D. insignis* in the U. S.: *Canis familiaris.*—Missouri (Elder, 1954); North Carolina (Dikmans, 1948); South Dakota (Benbrook, 1940); Texas (Turk, 1950). *Mephitis mephitis.*—Minnesota (Erickson, 1946). *Mustela cicognanii cicognanii.*—Minnesota (Goble, 1942). *Mustela vison.*—Iowa (Benbrook, 1940). (*Putorius vison*).—Nebraska (Chitwood, 1933). *Procyon lotor.*—Maryland (Chitwood, 1950); New York (Chitwood, 1933); Pennsylvania (?) (Leidy, 1858); Texas (Chandler, 1942). *Vulpes fulva.*—Iowa (Benbrook, 1932).

Dikmans (1948) reports that the U.S.N.M. Helminthological Collection contains specimens of *Dracunculus* from mink in New York, silver fox in Wisconsin and muskrats in Maryland and North Dakota.

It is of interest to note that Chitwood (1950) is the only author to report and describe the male *D. insignis.*—WILLIAM D. WILSON, Michigan State University, East Lansing.

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